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MUSKOX HABITAT AND USE PATTERNS
IN NORTHEASTERN ALASKA

A

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MUSKOX HABITAT AND USE PATTERNS

IN NORTHEASTERN ALASKA

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ABSTRACT

The habitat requirements of a rapidly expanding population of reintroduced muskoxen (*Ovibos moschatus*) in northeastern Alaska were studied. Of eight vegetation types described and mapped, muskoxen preferred riparian types where they used willow as a major component in their diet. Muskoxen also foraged heavily on forbs which were abundant during summer in the riparian areas. Above-ground, current season's growth for the willow, *Salix alaxensis*, peaked at 82.4 $g \cdot m^{-2}$. Forage species had high nutritive values and species diversity was high in the study area. The combination of these vegetative characteristics provided muskoxen with the opportunity to obtain a high quality diet and helps to explain the success of muskoxen along the Sadlerochit River. The strong fidelity of muskoxen for riparian habitat in northeastern Alaska and their associated high productivity point to the critical nature of riparian habitat to the future well-being of muskox populations.

ACKNOWLEDGEMENTS

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INTRODUCTION

Muskoxen, (*Ovibos moschatus*), although probably never abundant, were once distributed widely across the Arctic Coastal Plain of Alaska from at least as far west as the Kuk River south of Wainwright (Anonymous 1978), east to the Canadian border (Bee and Hall 1956). The introduction of firearms to the native peoples by whalers and arctic explorers during the 19th century and the purchasing of meat by these people while overwintering in the Arctic probably led to the extinction of the muskox in Alaska. Records indicate that the last muskoxen were killed in 1858 southwest of Barrow (Bee and Hall 1956).

In 1927, the Alaska Territorial Legislature requested the U.S. Congress to purchase muskoxen for husbandry experiments in Alaska (Bell 1931). It was thought that harvesting the muskox's soft, warm inner-wool, or "qiviut," from domesticated herds would provide an economically feasible cottage industry for Alaskan natives. In May 1930, the U.S. Congress appropriated $40,000 for this purpose, and later that year 34 muskoxen captured in Greenland were shipped to Alaska and held in captivity near Fairbanks (Bell 1931). After several years of experimental domestication work, lack of funds forced discontinuation of the project, and the 31 remaining muskoxen were released on Nunivak Island off the west coast of Alaska in 1935 and 1936. In March 1969, in order to relieve population pressure from the rapidly growing herd on the island and as part of an effort to reestablish muskoxen on the Arctic Coastal Plain, 51 muskoxen from Nunivak Island were released at Barter Island in the Arctic National Wildlife Refuge (ANWR). The following year, 13 more were transplanted near the Kavik River adjacent to the western border of the ANWR. The released muskoxen scattered, some moving east into Canada and others south onto the coastal plain or into the Brooks Range. Deaths occurred due to the rigors of the capture and handling and a few animals were shot by people unaware of the reestablishment effort.

One month after the 1969 transplant, however, five muskoxen were seen near Sadlerochit Springs (Lent 1971) (Figure 1), and thereafter a herd was frequently sighted along the Sadlerochit River (Roseneau and Stern 1974, Bente 1977, W. Audi pers. comm.). That this area of the ANWR might prove to be good muskox habitat is supported by observations of Bee and Hall (1956) who reported two historical records of muskox remains near the Sadlerochit River in 1886 in the Brooks Range and in 1934 at Anderson

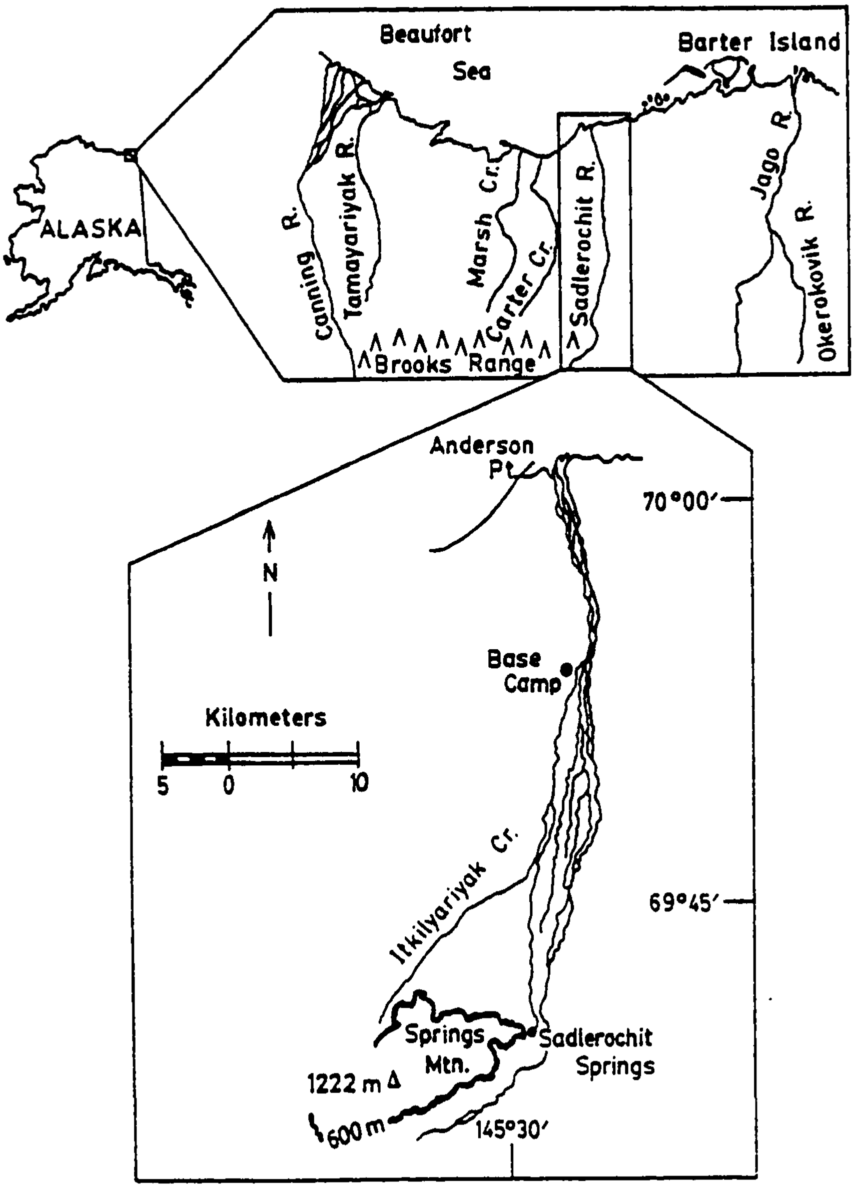


Figure 1. Location of the Sadlerochit River study area.

Point (Figure 1). Two other herds have established in the Canning-Tamayariak and Jago-Okerokovik drainages north of the Brooks Range as a result of the 1969-70 transplants (Figure 1). A population survey by personnel of the U.S. Fish and Wildlife Service in April 1980 revealed 148 muskoxen in three herds in the ANWR, including 54 muskoxen in the study herd on the Sadlerochit River (D. Ross pers. comm.). In May 1980, before final calving, there were 64 muskoxen in two groups on the Sadlerochit River (Jingfors 1980). The population production rate of this and other recently-established Alaskan muskox herds is amongst the highest ever recorded (Jingfors and Klein in prep.).

With the apparent success of the muskox transplants in arctic Alaska, it became increasingly important to define and describe their range, to assess their impact upon it, to establish their habitat requirements and to compare them with those of muskoxen elsewhere in other arctic regions. It was also necessary to investigate the possibility of competition with other native species for food and space. The North Slope drainage of the Sadlerochit River was selected to carry out this study because it was known to encompass the discrete range of a muskox herd descended from animals transplanted in 1969 and 1970. Familiarity with the area and background information available as the result of my involvement in a vegetative reconnaissance during the summer of 1977 (Nodler 1977) assisted in designing this study.

The first objective of this study was to delineate and describe the habitat used by reintroduced muskoxen in the Sadlerochit River drainage. Vegetation of northern Alaska has been described before by several authors. Spetzman (1959) identified plant species and described community types for the mountains, foothills and coastal plain of northern Alaska. However, no data were collected from the eastern North Slope. Spetzman described six communities for the Alaskan Arctic Slope. He included a Floodplain and Cutbank Community which was a broad class and included all riparian habitats. These riverine habitats are important to the muskoxen in the Sadlerochit River area and I found it necessary to break down Spetzman's riparian community further. Intensive investigations of vegetative patterning have been made in coastal tundra near the Beaufort Sea at Prudhoe Bay (Neiland and Hok 1975, Webber and Walker 1975) and at Barrow (Webber 1978). However, vegetation of the Sadlerochit River area was more typical of the nearby foothills and mountains. In contrast, vegetation at Prudhoe Bay and Barrow is more reflective of the flat, wet, graminoid-dominated tundra of the Coastal Plain. Nodler

(1977) described plant communities for the North Slope of the ANWR using LandSat infrared imagery. Thirteen major community types were identified based on cluster class analysis. Communities have also been described for the Seward Peninsula, Alaska and Northwestern Alaska using LandSat information (Nodler *et al*. 1978).

Some problems arise when dealing with satellite imagery. In the analysis of the digitized data, the assumption is made that vegetated areas reflecting similar light intensities are composed of similar plant species. Distortions in light reflectancies, however, may occur as artifacts of atmospheric haze and cloud and terrain shadows. Although some of these distortions may be eliminated through field identification of the vegetation classes, it can still contribute substantial error to plant type description. Murray and Batten (1977) have also described tundra communities for the Alaskan Arctic. Viereck and Dyrness (1980) developed a hierarchical system for tundra and shrubland based on Murray and Batten's classifications. Based on the classification scheme used by Nodler (1977), the communities described in the present Sadlerochit River study are identical to many of the types described by Viereck and Dyrness.

Another objective of this study was to produce a vegetative map of the range used by the muskox herd. Arctic vegetation has been mapped at a detailed scale by Webber and Walker (1975) and Webber (1978). Vegetation along the Trans-Alaska Pipeline Haul Road has also been mapped in a similar manner (Brown and Berg, eds. 1980). Mapping at this scale facilitates understanding the complex relationships within plant communities and provides reference material for future plant and soil studies. However, this intensity of mapping was not necessary for the assessment of muskox habitat and was therefore outside the scope of this study. Vegetation mapped on a broader scale, as in this study, locates major vegetation types and therefore assists in understanding their importance to animal populations' distributions and use. In addition, use can be made of satellite imagery and high level aerial photography for such large scale mapping, where the resolution is too coarse for such intensive studies as previously mentioned.

A third goal of this study was to identify important muskox forage species and note the seasonal progression of use. Information on muskox forage use in other areas is available from a variety of sources: Tener (1965), Bos (1967), Spencer and Lensink (1970), Lent and Knutson

(1971), Alendal (1974), Hubert (1974), Wilkinson *et al*. (1976), Ferns (1977), Parker (1978), Roby (1978 *b*) and Jingfors (1980, pers. comm.). However, use in relation to vegetation classification and productivity for northern Alaska has not previously been reported. Therefore, muskox food habits will be dealt with in greater detail in the discussion of forage preferences.

The final objective of the study was to examine the productivity of the range and relate quality of forage to seasonal use by muskoxen. Herbivores depend on primary production for their nutritive needs, and a productive community may be able to support more consumers than a similar habitat with poorer availability and quality of forage. A hypothesis to be tested in the study was that good quality range was the basis for the observed high productivity of the Sadlerochit muskoxen. Investigations of plant productivity in the Arctic have been reported by Bliss (1956, 1962, 1971), Haag (1974), Wein and Bliss (1974), Chapin (1978), Chapin *et al*. (1980), and Wielgolaski (1980). My approach was to measure the above-ground plant standing crop (biomass), nutrient quality and diversity of forage species available to muskoxen on the Sadlerochit River study area and to compare these parameters with those of other arctic regions.

STUDY AREA

The Sadlerochit River study area covers a 40 km strip along the Sadlerochit River on the Arctic Coastal Plain of the ANWR from the coast of the Beaufort Sea (70°01') to several km south of Sadlerochit Springs (69°37') (Figure 1). The area is wide enough to include most of the territory in which muskoxen have been sighted since the 1969 transplants. At its widest, the western boundary extends close to Carter Creek (144°42'). The eastern boundary is only about 2 km from the river (144°17').

Climate

Weather data collected by the National Weather Service at Barter Island during the two years of study are shown in Figure 2. Barter Island weather is influenced by its marine surroundings and does not accurately reflect the climate of the study area. Temperatures are likely to be warmer in the summer, wind velocities lower and the precipitation slightly greater in the Sadlerochit River area. The difference in temperatures between coastal and inland locations has been discussed by Brown _et al_. (1975) and Brown and Berg, eds. (1980). Temperatures are clearly

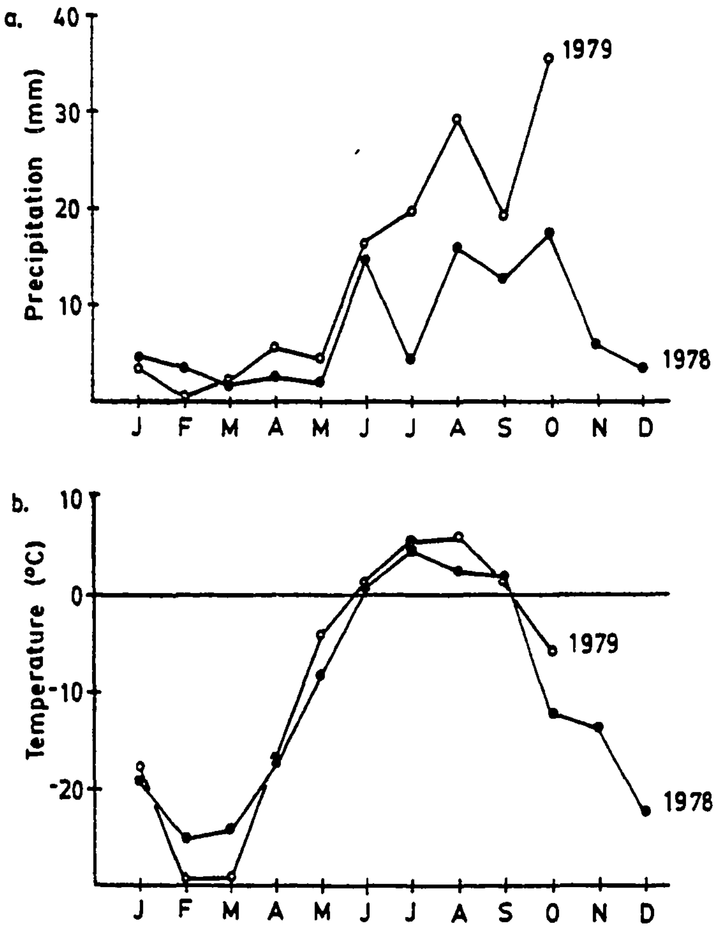


Figure 2. Mean monthly temperatures and total monthly precipitation for 1978 and 1979, Barter Island, Alaska. From Anonymous (1978 a, 1979).

warmer at the more inland stations than at the coastal locations of Prudhoe Bay and Barter Island (Table 1). The winter climate may not differ as much between inland and coastal locations as in the summer because the Beaufort Sea is frozen and the maritime influence is thus minimized. Wind velocities, however, do decrease inland during winter, as is typical of this high latitude area. These aspects are discussed in more detail by Searby and Hunter (1971).

Geology

The Arctic Coastal Plain is made up of Quaternary sediments laid over Cretaceous bedrock which has been modified since the last Wisconsin glacial transgression (Murray 1978). Murray discusses this in detail and the reader is referred to his work and that of Brown and Sellmann (1973) and Hartman (1973) for more information on the geologic history of the area.

The topography is relatively featureless, being representative of the terrain north of the Brooks Range. Tundra on either side of the river is underlain by permafrost and the land shows typical ground features caused by seasonal frost action: polygons, frost boils and upheavals and meadows of tussock-forming graminoids. Some

Table 1. Mean monthly temperatures (C) at coastal and inland locations for June, July and August 1972 and 1973. From Brown *et al*. (1975).

Location	Distance from coast (km)	Mean monthly temperature June	July	August
1972				
Barter Island	0	1.2	4.1	5.2
Prudhoe Bay	0	2.7	6.3	5.7
Franklin Bluffs	16	2.5	7.3	6.5
Happy Valley	130	8.1	12.6	9.8
1973				
Barter Island	0	1.2	4.9	4.3
Prudhoe Bay	0	2.2	6.8	6.4
Happy Valley	130	8.7	12.2	7.5

low-lying ridges of elevations up to 130 m occur, especially in the northwestern part of the study area. The base camp was located near the river 16 km south of the Beaufort Sea coast at an elevation of about 76 m. The southern extent of the study area includes part of the eastern-most mountain of the Sadlerochit Range which rises to 1222 m, hereafter referred to as Springs Mountain (Figure 1).

Much of the low-lying ground is poorly drained and standing water is common from late May through June when the upper layers of the soil are still frozen. In the more hilly terrain, gullies provide drainage during spring runoff. These streams, although torrential for a period of ten days to two weeks, are seasonal and become dry by July when most of the snow has melted. Some small lakes are present in the study area and are ice-free by mid-July.

Sadlerochit Springs issue from the north base of Springs Mountain and flow year round. In June 1979 the water temperature was 12.7 C which was considerably warmer than the water temperature in the nearby river. Several streams run north from the Springs and associated seepage, merge and finally flow into Itkilyariak Creek which drains into the Sadlerochit River near the base camp location. A large field of "aufeis" resulting from the creek's overflow in the winter forms 5 to 6 km north of the Springs and persists through late summer. The flora is lush at the Springs and is difficult to classify into vegetation types typical of the Coastal Plain. Birds common further south in the Brooks Range are found here but not in other parts of the study area.

Flora

The Arctic Coastal Plain was unglaciated during the Pleistocene and probably served as a refugium for many plant species (Hultén 1968). Murray (1978) also reviews the floristic history and plant biogeography of the Arctic Coastal Plain. The flora is well represented by low alpine and arctic plants which are adapted to cold and windy environments. Shrubs (*Salix spp.*) may grow to 2 m in the river drainage in the southern portion of the study area and in sheltered areas on the south-facing slopes of gullies.

Those species that occurred only at Sadlerochit Springs were: *Populus balsamifera* (the only tree in the study area) which reached 2 to 3 m, *Dryopteris fragrans*, *Zygadenus elegans*, *Delphinium glaucum*, *Aconitum* delphinifolium subsp. delphinifolium, Corydalis pauciflora, Chrysosplenium wrightii, Spiraea beauverdiana, Geum macrophyllum subsp. perincisum, Shepherdia canadensis, Epilobium angustifolium subsp. angustifolium, Pedicularis labradorica, Pinguicula vulgaris subsp. vulgaris, Linnaea borealis subsp. borealis and Achillea borealis.

Vegetation of the area will be discussed in more detail in the chapter on range characteristics.

Fauna

The animal life in the study area is also adapted to a cold environment. Some species are migratory and are not present during the colder months and others are present but are not active in the winter. The muskox is one of the species that is active in the study area year round. Other species active in the winter include arctic foxes (Alopex lagopus), wolverines (Gulo gulo), wolves (Canis lupus), and ermines (Mustela ermina). Red foxes (Vulpes vulpes) have been seen on occasion in the southern part of the study area. Polar bears (Ursus maritimus) may be present in the study area, but are rare visitors and would be present only in the winter. Brown bears (Ursus arctos) are active only in the warmer months and moose (Alces alces), often seen near Sadlerochit Springs and occasionally further north, probably winter south of the study area. Caribou (*Rangifer tarandus*) of the Porcupine Caribou Herd migrate through the study area and are most abundant from late May through June, but may be seen there before May and until September. Dall sheep (*Ovis dalli*) are present on Springs Mountain. Tundra voles (*Microtus oeconomus*), northern red-backed voles (*Clethrionomys rutilis*), collared lemmings (*Dicrostonyx torquatus*) and brown lemmings (*Lemmus sibiricus*) remain in the study area in the winter and are active beneath the snow. Arctic ground squirrels (*Spermophilus parryii*) are present but hibernate during winter.

Most of the avifauna leave the area in the winter; but, by late April, willow ptarmigan (*Lagopus lagopus*) and rock ptarmigan (*L. mutus*) are quite abundant and feed heavily on willow buds (*Salix* spp.) above the snow and may be important competitors for food with muskoxen. Detailed information on bird life in the Arctic Coastal Plain and the Brooks Range has been reported by Sage (1974) and Salter *et al*. (1980).

METHODS

Range Description

I divided the vegetation of the study area into eight major types. A representative area of at least 1 ha was then sampled using 30 m transects with 0.5 m^2 quadrats at 1 m intervals. Percent cover of each plant species was estimated in each quadrat. The averages of plant species cover were used to describe the eight types.

A range map was constructed using NASA high-level infrared aerial photography from 1978 and 1979 provided by the Geophysical Institute at the University of Alaska. After identification and sampling of range types, 200 random points were selected over the study area and located on U.S.G.S maps at a scale of 1:63,360, the same scale as the photographs. The range type for each point was identified by careful examination of the photographs. Areas (A) for each vegetation type were calculated using the number of points (p) that fell into that type out of 200 and multiplying that value by the total land area (28,487 ha).

$$A = p/200 \times 28,487 \text{ ha}$$

Vascular plant species were collected intensively within 1 km of the base camp location on the Sadlerochit River during 1978 and 1979, and are listed in Appendix A. Herbaceous vascular plants were identified using Hultén (1968) and woody species using Viereck and Little (1972). Spelling of plant species names follows currently accepted usage. References used for cryptogams were Conard (1956) and Dahl and Krog (1973).

Forage Use and Preference

A total of 12 feeding sites were sampled to determine muskox forage use: 2 in July 1978 and 10 from late May through August 1979. A feeding site was sampled as follows: Three 30 m transects were randomly placed within a recently used feeding area. At 1 m intervals a 0.5 m^2 quadrat was placed along the line. Within each plot percent cover of plant species or groups of species present was recorded. The percent cover taken by foraging muskoxen was estimated by a comparison of clipped with unclipped vegetation. Notes were taken in reference to what plant parts were being removed. From this information preference ratios were calculated as described below.

Total area covered by the transects within a site was 45 m^2 (90 x 0.5 m^2). Availability of plant species x was calculated by summing the total amount of area covered by species x on the transects (A_x). Availability per m^2 (a_x) was calculated by dividing A_x by 45 m^2. Total amount of species x removed by muskoxen (G_x and g_x) was calculated in a similar manner. Next the relative availability of species x (RA_x) was expressed as a percentage of the sum of the availability of all species, n ($a_x / \sum_{i=1}^{n} a_i$). Amount grazed for species x was then expressed as a percentage of the total amount grazed of all species, n ($g_x / \sum_{i=1}^{n} g_i$), to give a relative use fraction (RU_x). Finally, for each species, this last value was divided by the availability percentage, resulting in a preference ratio (PR).

$$PR = RU_x / RA_x$$

Ratios greater than one indicate that the animals fed on a species in greater proportion than it was available. A forage species was discriminated against when the ratio was less than one.

Winter information was restricted to cursory examination of feeding craters in May 1978 and March 1979. Kent Jingfors provided food habits information for October and November 1978 and for March and November 1979.

Fresh fecal samples were collected throughout the field study period and were pooled by season and analyzed for percent relative density of plant fragments at the Composition Analysis Laboratory at Colorado State University, Fort Collins.

Range Productivity

Three aspects of productivity were examined: above-ground biomass of representative forage species, nutrient concentration of 16 plant species and plant species diversity at the study site.

Biomass production was measured by weighing the current season's growth produced by a species at eight times during the summer from early June to early September. Band transects were located in representative areas; at 10 day intervals during the early summer and at 20 day intervals in late summer the above-ground parts of eight important plant species were collected at these sites. The current season's growth was expressed as dry weight per species per m^2. I noticed that one species (*Salix planifolia*) seemed to exhibit different levels of production as a consequence of vegetation type. Therefore it was sampled for green dry weight per m^2 in two vegetation types: a relatively productive one and one in which the plant exhibited poorer growth. The Kruskal-Wallis test (Conover 1971) was used to test the difference of the species means at 22 July (α=0.05).

Quality of the vegetation available to and taken by muskoxen was evaluated by examining the nutrient level of 16 plant species characteristic of the Sadlerochit area. Some of these were important forage species and some were not eaten by muskoxen. Plant foliage (current growth) was picked in a specific location for each species at 10 and 20 day intervals throughout the summer. Plants were air-dried in the field and later oven-dried in the laboratory at 70 C, ground in a Wiley mill and sent to the Plant Laboratory at the Agricultural Experiment Station in Palmer, Alaska for analysis of percent nitrogen, phosphorus and calcium content.

Species diversity at the Sadlerochit River area was compared with that of Prudhoe Bay, Barrow and Nunivak Island in order to determine whether the study site offered a greater variety of forage species to muskoxen. Species were grouped into four categories: graminoids (grasses and grass-like plants), forbs (the remainder of the herbaceous vascular plants), dwarf shrubs (woody species < 0.1 m) and shrubs (woody species > 0.1 m) and compared on this basis. The number of species within genera found to be heavily used by muskoxen in the Sadlerochit drainage were also compared with the number of species of these important genera present in the other areas.

RESULTS AND DISCUSSION

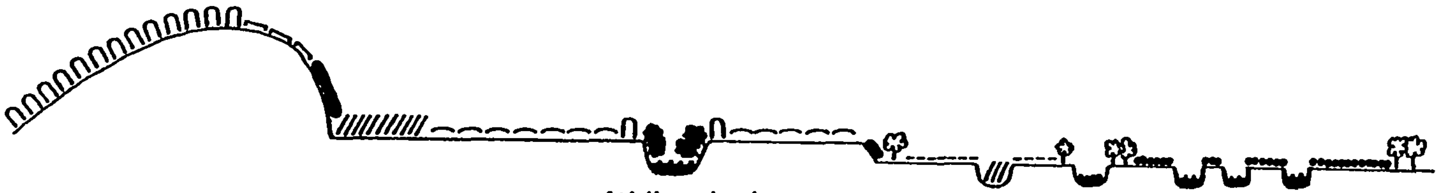
I. RANGE DESCRIPTION

Vegetation in the Sadlerochit River study area was divided into eight major types on the basis of physiognomy and the dominance of important plant species. These types were: Riparian Gravel Bar, Riparian Willow Thicket, Riparian *Dryas* Terrace, Wet Sedge Meadow, Heath-Polygon Tundra, Tussock Meadow, Dry Ridge and Creek Willow Thicket. The Creek Willow Thicket type was not distinguished from the other riparian habitats until after field investigation, and description of this type is therefore entirely subjective. Some small communities, such as localized snowbeds, were too small and infrequent to locate on the photographs. Of the eight vegetation types, seven were mapped. Riparian Willow Thicket and Riparian *Dryas* Terrace were combined because of their similar light reflectancies and close proximity to one another.

A. RIPARIAN HABITAT

Riparian Habitat covered about 20 % of the study area or approximately 5,700 ha (Figure 3). The Sadlerochit River is a "braided" arctic river made up of several entwining channels. Gravel bars are a characteristic of this area as a result of glacial outwash and stream erosion. The riparian area is normally inundated with water during flooding, and during late May through mid-June spring runoff is typified by swift flowing water carrying ice floes and debris. New river channels may be cut from year to year and new gravel bars created. Ice action in the winter may heave up mounds of gravel and contribute to changes in the system. Input of nutrients is great in comparison with other arctic vegetation types because of the flooding action each spring. Invasion of new habitats is facilitated by chunks of sloughed off stream banks, seeds and plant parts that have been swept downriver and which eventually beach on new sites. Plants of the legume or pea family (Leguminosae), including such genera as Astragalus, Oxytropis, Hedysarum and Lupinus, were commonly found in these areas.

Riparian Habitat was heavily used by muskoxen, especially during summer when the leguminous forbs were blooming and young willow growth was abundant. Riparian Habitat was made up of three vegetation types representing different successional stages: Riparian Gravel Bar,



Hectares	Percent of Study Area	Symbol	Vegetation Type
—	—		Snowbed
1420	5.0		Water
2140	7.5		Riparian Gravel Bar
3560	12.5		Riparian Willow Thicket
			Riparian *Dryas* Terrace
2560	9.0		Wet Sedge Meadow
2850	10.0		Heath-Polygon Tundra
1280	4.5		Dry Ridge
13680	48.0		Tussock Meadow
997	3.5		Creek Willow Thicket
28487			

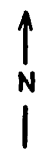


Figure 3. Transect approximately 1 km, west to east, showing vegetation types at the base camp location, Sadlerochit River.

Riparian Willow Thicket and Riparian Dryas Terrace.

Riparian Gravel Bar

Gravel bars covered 37.5 % of Riparian Habitat and 7.5 % of the study area or about 2,140 ha. These were islands of glacial rubble in and along the river, and this type was the most disturbed in the study area. Gravel bars were often less than 50 % vegetated, and debris and mud were common. Water rose and fell periodically during the summer season, depending upon the frequency and amount of rainfall south of the study area in regions drained by the Sadlerochit. Water levels also rose on warm, sunny days from increased glacier melting in the mountains. Gravel bars were often either "high and dry" or inundated. This factor can account for additional stress on the plants. Many of the plants that occurred here were pioneering species common to recently disturbed ground. The most abundant plant was Astragalus alpinus which had an average cover of 22.2 %. An additional 23.1 % cover was made up by various grasses, Salix alaxensis, Epilobium latifolium, Oxytropis maydelliana, Hedysarum mackenzii, Artemisia arctica subsp. comata, Oxytropis deflexa and Stellaria spp.

The combined Riparian Willow Thicket and Riparian

Dryas Terrace types comprised 62.5 % of Riparian Habitat and 12.5 % or 3,560 ha of the study area (Figure 3).

Riparian Willow Thicket

Riparian Willow Thicket was found in association with the gravel bars. This type was successionally more advanced and less disturbed than the Gravel Bar type. Vegetation was more continuous although bare patches of gravel were still quite common. This type was less influenced by the dramatic changes in the river course and species associated with secondary succession were common here. *Salix alaxensis* was the most abundant species with an average cover of 22.7 %. Although abundant throughout all riparian habitats, *S. alaxensis* flourished in this vegetation type and muskoxen fed heavily on this species in this type. In the southern part of the study area *S. alaxensis* reached heights of 3 m. Further north, willow decreased in size and near the base camp they rarely reached 1.5 m. Near the mouth of the river willows were sparse and the growth form quite low. A ground cover of 35.9 % was attributed to grasses, *Salix glauca*, *Oxytropis borealis*, *Hedysarum mackenzii* and *Lupinus arcticus*. Gravel, sand and mud made up about 25 % of the surface area.

Riparian Dryas Terrace

The final riverine vegetation type was common on both banks of the river in and adjacent to old river channels. Dryas Terrace was characterized by dry, flat vegetated ground over an underlying layer of gravel. It was commonly intermingled with the willow thickets. The terrain was often cracked from frost action. This type was only disturbed by the river when it occurred on banks alongside the main, active channels. Here, slabs of earth and vegetation were undercut and would eventually slough off and be carried downstream leaving more exposed soil to erode. Sloughing banks were common along the steeper shores of the river where water and weather wore down the exposed earth. Due to the underlying gravel substrate, the terraces were well drained and dry. Terraces may become quite extensive along rivers draining the north slope of the Brooks Range but they are not well developed along the Sadlerochit, the Riparian Willow type being much more prevalent. As in the other two riparian types, terraces were usually flooded during spring runoff. Mosses (primarily Pleurozium schreberi, Politrichum spp. and Dicranum spp.) had an average cover of 42.8 % and Dryas integrifolia, Carex spp., Astragalus umbellatus, Salix reticulata, Arctostaphylos rubra and Equisetum variegatum made up a further 50.0 %. Very little of the ground was unvegetated.

B. MESIC TUNDRA

Further from the river, vegetation was less disturbed and communities tended to be of a climax type. Mesic tundra made up 19.0 % of the study area or 5,410 ha.

Mesic Tundra did not include many species favored by muskoxen and the animals were therefore rarely seen in these areas. Two vegetation types comprised Riparian Habitat: Wet Sedge Meadow and Heath-Polygon Tundra.

Wet Sedge Meadow

Wet Sedge Meadows covered 9.0 % of the study area or 2,560 ha and 47.4 % of Mesic Tundra. This community type was located on poorly drained ground, old slough and lake beds and around the margins of ponds. These areas are flooded during spring and do not drain appreciably. Standing water is characteristic of sedge meadows during late May, June and early July. By mid-July, the height of the growing season, much of the water has either evaporated or been absorbed by the warming earth. Often the ground is moist if no standing water is present. Mosses (Pleurozium schreberi and Sphagnum spp.) had an average cover of 44.7 % and Carex aquatilis, Salix planifolia, Potentilla palustris, Dupontia fischeri and Eriophorum angustifolium contributed an additional 29.8 %. Much of the cover consisted of dead plant litter, especially the old leaves of Carex aquatilis, Eriophorum angustifolium and Dupontia fischeri.

Muskoxen rarely fed in Wet Sedge Meadows, and only did so when they were close to Riparian Habitat. Salix planifolia was the only important forage species in this type.

Heath-Polygon Tundra

Heath-Polygon Tundra covered about 10.0 % of the study area or 2,850 ha and 52.6 % of Mesic Tundra (Figure 3). This type was located on the higher plateaus near the river and was often distinguished by indefinite to well-formed high-center polygons caused by frost action. Intermingling with wet sedge meadows was common. Occasionally polygon troughs contained standing water and were surrounded by boundaries of microhabitats of wet sedge. This was included in the verbal description of the type but not in the sampling. Ericaceous plants were conspicuous. The soil was quite organic and peaty down to permafrost and below. Mosses (Politrichum spp., Ceratodon purpureus and Dicranum spp.) were the most common plants with an average cover of 54.8 %. Betula nana, Vaccinium vitis-idaea, Carex bigelowii, Salix planifolia, lichens (Dactylina arctica, Cetraria spp., Thamnolia vermicularis and Peltigera spp.) and Dryas integrifolia accounted for an additional 46.1 % of the cover.

Heath-Polygon Tundra was used by muskoxen when it was near Tussock Meadow or when it was associated with the riparian areas. Salix planifolia was the most important species grazed, but muskoxen also fed on Peltigera spp. in this type during spring.

C. DRY TUNDRA

Dry Tundra was made up of two vegetation types totalling 52.5 % or 14,960 ha of the study area. Dry tundra was common on either side of the river drainage. Water was present only in small, local depressions which might catch spring runoff and these were usually dry by mid-July.

The two vegetation types which comprised this category, Tussock Meadow and Dry Ridge, provided food items such as *Eriophorum vaginatum*, *Salix planifolia* and *Dryas integrifolia* for muskoxen during spring. Calving occurred in a large, upland valley west of the Sadlerochit River in 1978 and 1979, and muskoxen found ample food in this large, dry area during this time when the riparian habitats were flooded.

Tussock Meadow

Tussock Meadow was the most extensive vegetation type, accounting for 91.4 % of Dry Tundra and 48.0 % of the study area or 13,680 ha (Figure 3). This type was located on well drained grades on the low hills several km from either side of the river. Strips of wet sedge meadow were present in slight depressions and gullies that drained water during spring break-up. *Eriophorum vaginatum* was the most conspicuous species and formed the tussocks. These tussocks were about 0.2 m high and sometimes taller. Tussock Meadow also had an abundance of low shrubs found in the Heath-Polygon type. Two larger shrubs, *Salix planifolia* and *Betula nana*, were quite prevalent, growing between the tussocks. During spring break-up, water ran down the slopes and the ground was icy and wet. As the summer progressed the top 0.1 m thawed and contributed more moisture between the tussocks and in flat areas and basins. By mid-July much of the area was dry and standing water was present only in small, infrequent depressions. Mosses (Pleurozium schreberi, Sphagnum spp. and Politrichum spp.) had an average cover of 58.2 %. Carex bigelowii, Salix planifolia, Eriophorum vaginatum, Vaccinium vitis-idaea, and Salix phlebophylla accounted for an additional 43.0 %.

Dry Ridge

The Dry Ridge type made up a small part of the study area comprising only 8.6 % of Dry Tundra and 4.5 % or 1,280 ha of the study area (Figure 3). This type was restricted to small, local strips on the crests of the more pronounced ridges on the Coastal Plain but was quite common in the mountainous terrain in the southern portion of the study area. Bare ground and rubble were common in the patches of Dry Ridge type on the Slope and talus scree was more prevalent in the mountains. Frost boils were common, often forming a patchwork of earth and small rocks. Fissures in the ground were also common due to frost action. Dryas integrifolia was the most common species with an average cover of 39.2 %. Salix phlebophylla, Luzula tundricola and

Oxytropis nigrescens made up an additional 19.0 %. Bare ground and rubble covered up to 30 % of the sampled area.

D. MISCELLANEOUS TYPES

Creek Willow Thicket

Creek Willow Thickets were relatively rare comprising only 3.5 % of the study area or 997 ha (Figure 3). Willows often occurred in sheltered places along the creeks that drained into the Sadlerochit River. These were in small, local pockets and grew 2 to 3 m tall. The undergrowth consisted of more sedges and fewer leguminous forbs than in the Riparian Willow Thicket type. Soil instead of gravel composed the substrate and probably accounted for the different undergrowth. Steep banks sheltered much of this habitat type and snowbeds were common through most of July. Predominant plants were *Salix planifolia* and *Salix lanata*.

Creek Willow Thickets were often heavily used by muskoxen, especially when the willow thickets grew in crevices along small streams leading down to the river, or when they occurred in gullies in the rolling tussock tundra. Forage species included *Salix lanata* and *S.*

planifolia. Forbs, such as those found in the riparian areas, were also heavily grazed.

Water

Water, primarily lakes, stream drainages and the Sadlerochit River, made up the remaining 5.0 % of the study area or 1,420 ha (Figure 3).

A range map of the Sadlerochit River study area is presented in Figure 4.

In general, muskoxen preferred the riparian and creek habitat types where willow and forbs were abundant. The Dry Ridge and Tussock Meadow types were used in May and June when the riparian types were flooded. Wet Sedge Meadow and Heath-Polygon types were rarely used.

II. FORAGE USE AND PREFERENCE

Use of forage items is governed by complex preference-availability relationships, where availability depends upon abundance of food, its distribution, conspicuousness and other factors (Dirschl 1969). In reality, much of a food plant is not normally consumed by

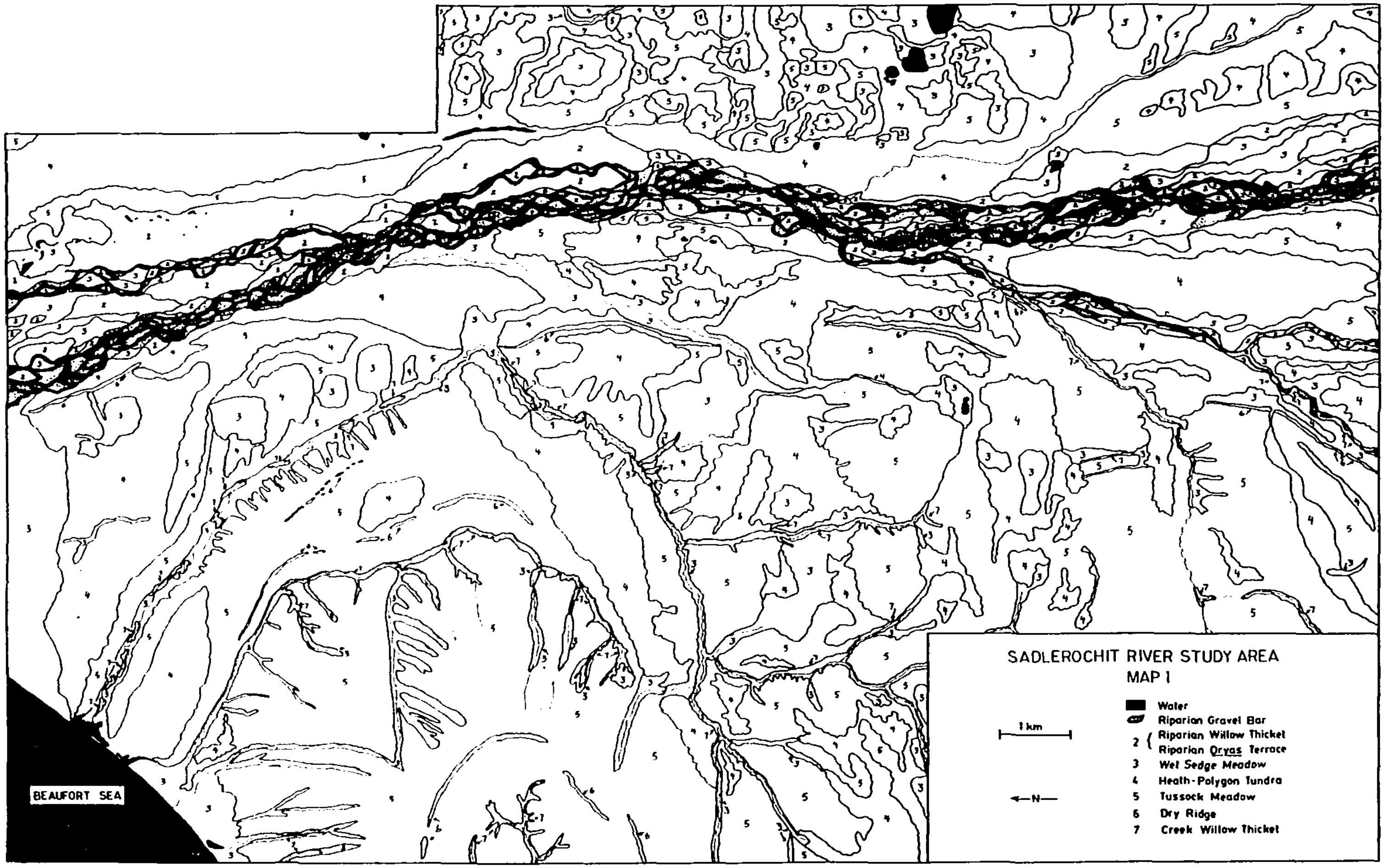


Figure 4. Range Map 1 of the Sadlerochit River study area. Based on U.S.G.S. NASA aerial photographs.

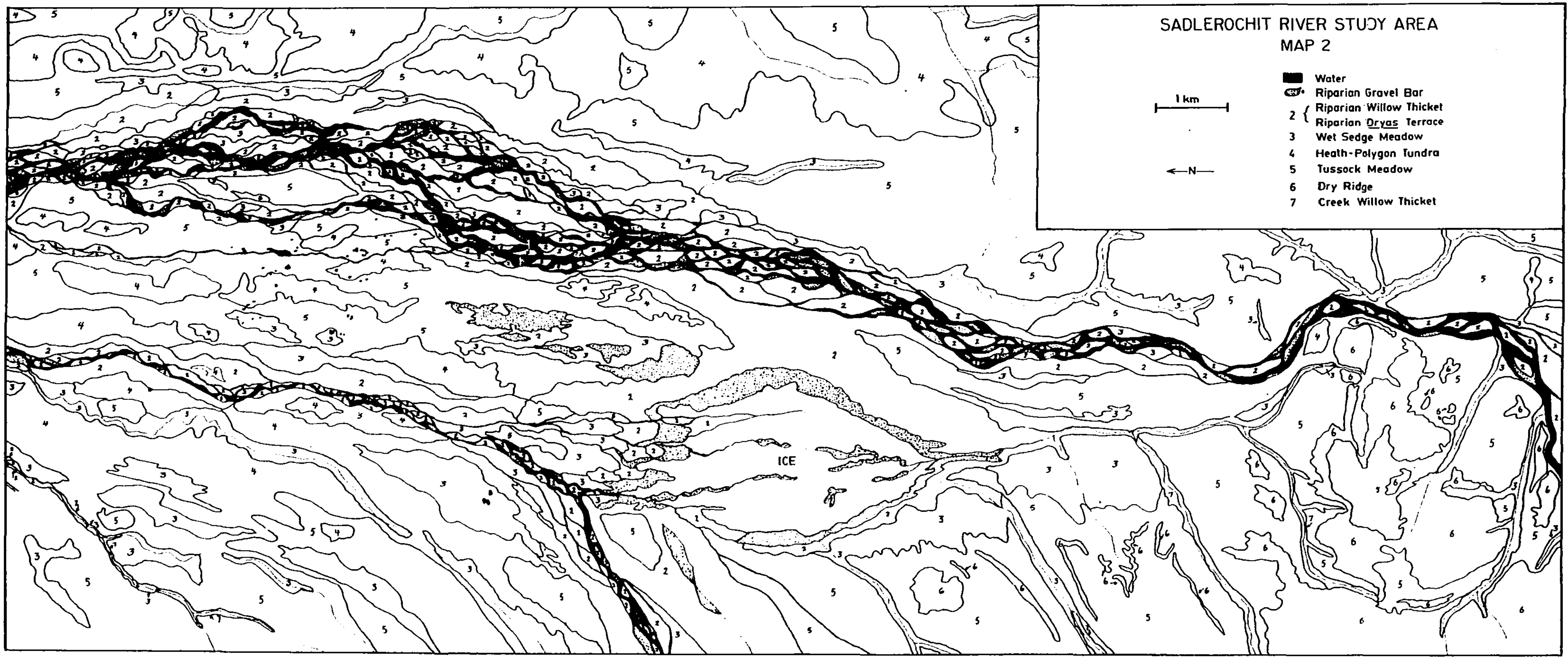


Figure 4. (cont.) Range Map 2 of the Sadlerochit River study area.

an herbivore because only part of the plant is preferred forage and other parts are not readily available during the normal course of feeding. This is especially true of willows, where a large proportion of the plant is woody material, but only the green shoots and leaves are eaten in the summer. In the winter when twigs are eaten it is primarily the newest growth that is taken in preference to older stems with a higher proportion of woody tissue. When measuring availability in the field, however, it was most feasible to include ground cover of the entire plant. Whenever possible I noted which plant parts were being selected and these will be discussed later.

Use of forage will also vary according to the status of the range and its herbivores. A plant that is normally taken in one area may not be taken in another because of overgrazing, inaccessibility or for other reasons. In such situations species may be fed upon that would not otherwise be considered important.

Preference Ratios

In general, grasses and sedges were selected against by foraging muskoxen in the Sadlerochit River area (Figures 5 and 6a). *Eriophorum vaginatum*, however, was an important

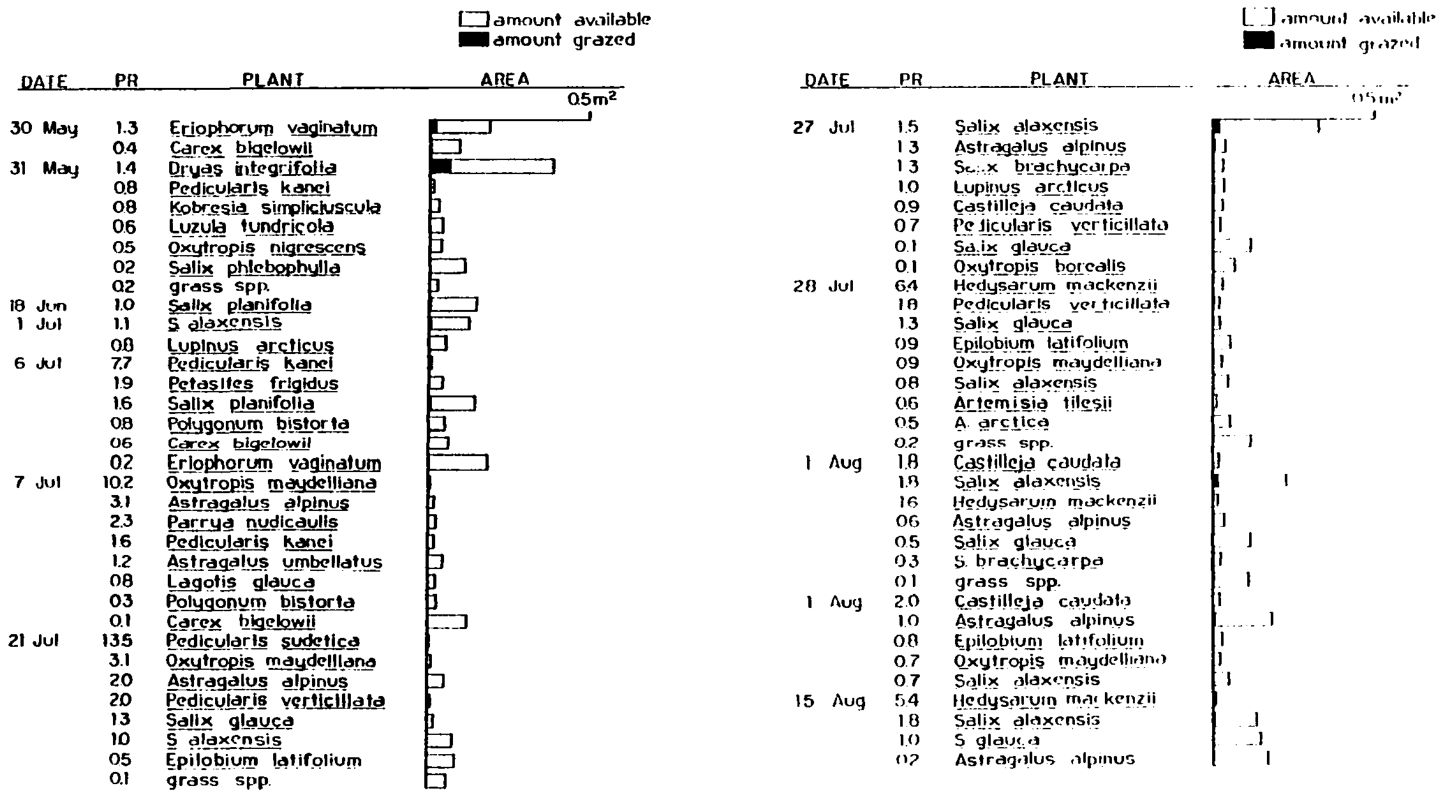


Figure 5. Preference ratios for species grazed by muskoxen during the growing season and the relationship between the amount available and amount grazed expressed as area.

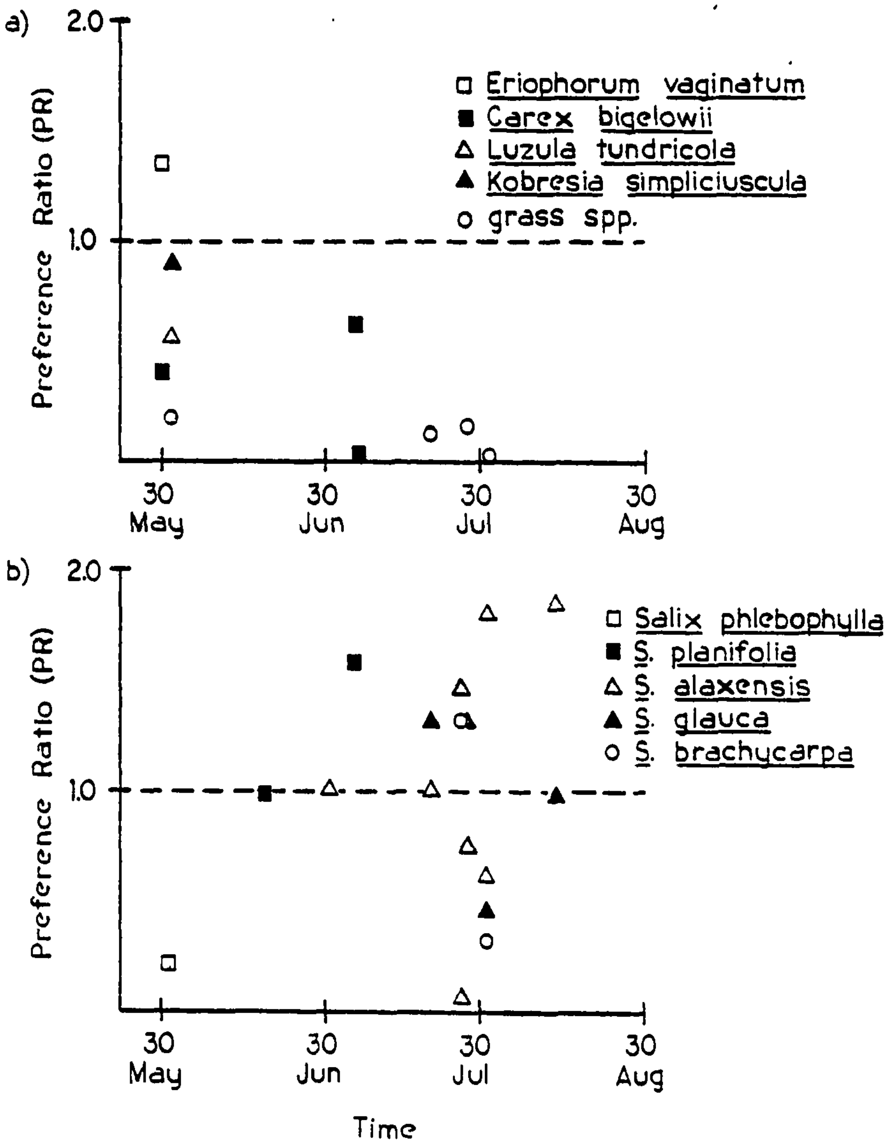


Figure 6. Preference ratios during the growing season for: a) graminoids and b) willow.

food item in late May and was selected during this time (PR=1.3), although later in the summer *E. vaginatum* was selected against (PR=0.2).

Willows were selected throughout most of the growing season with increasing use as the summer progressed but never with extremely high ratios (Figures 5 and 6b). *Salix phlebophylla* was eaten in late May in snow-free areas, although it was discriminated against at this time (PR=0.2). *S. planifolia* (PR=1.0) was eaten in relation to availability in early summer. As riparian willows initiated growth they became important food items, especially *S. alaxensis*, which was often taken in excess of availability (PR=1.1, 1.5, 1.8 and 1.8), as was *S. glauca* (PR=1.3 and 1.0) and *S. brachycarpa* (PR=1.3). Willows are very abundant in the study area throughout the growing season and are eaten in greater proportion than their availability through most of the growing season.

With few exceptions, forbs are not available early in the growing season. *Pedicularis kanei* (PR=0.8) and *Oxytropis nigrescens* (PR=0.5) appear before complete snowmelt, but they were not selected for (Figures 5, 7a and 7b), and young willow and *Eriophorum vaginatum* were more important in the diet at this time. By early July, many

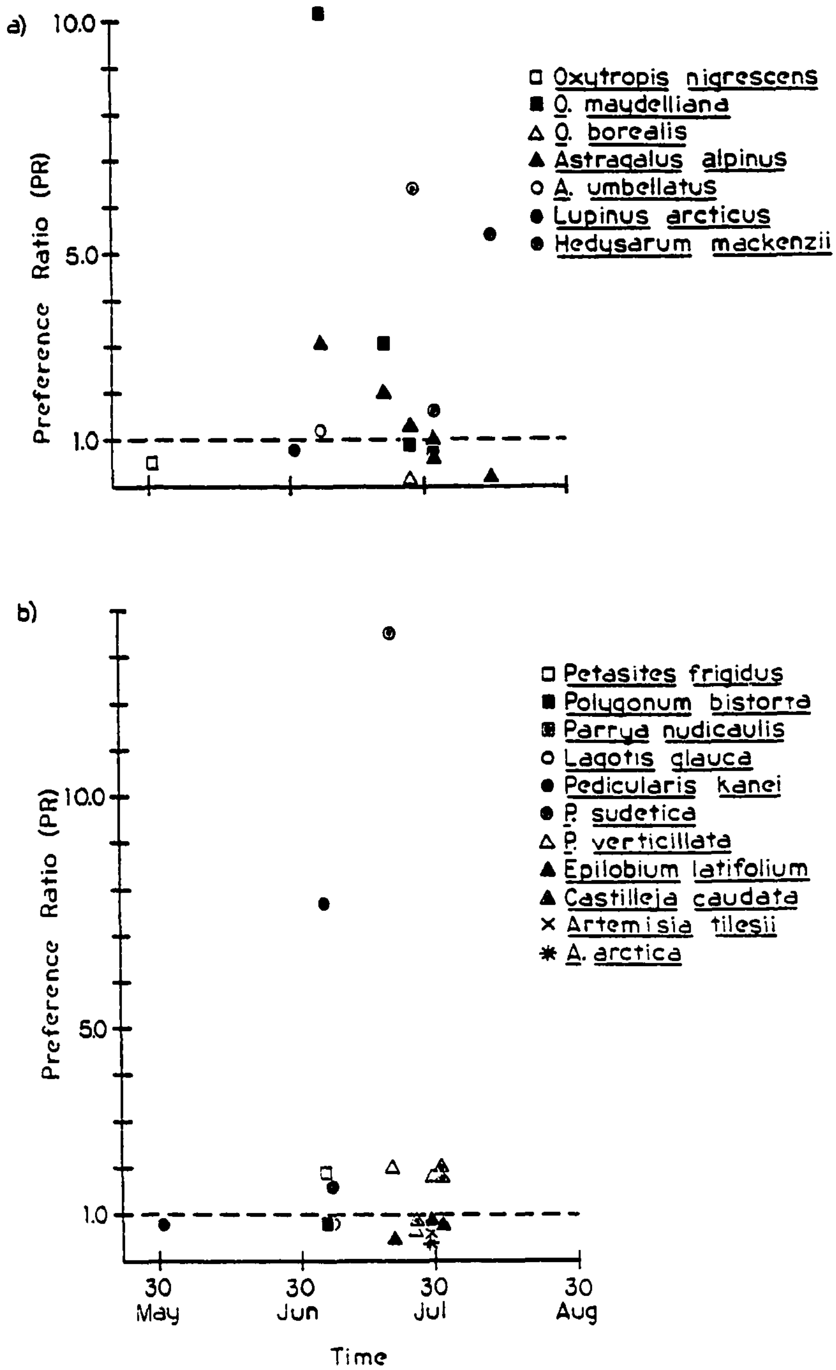


Figure 7. Preference ratios during the growing season for: a) seven leguminous species and b) 11 other forbs.

forbs were blooming and muskoxen were selecting such species as _Petasites frigidus_ (PR=1.9). Some forbs were present in small amounts but were highly selected for, resulting in extremely high PR values. These included: _Oxytropis maydelliana_ (PR=10.2) and _Pedicularis sudetica_ (PR=13.5). Other forb species had relatively high PR values: _Astragalus alpinus_ (PR=1.3 and 1.1), _Hedysarum mackenzii_ (PR=6.4, 1.6 and 5.4), _Pedicularis verticillata_ (PR=1.8) and _Castilleja caudata_ (PR=1.8 and 2.0). Throughout July and early August forbs were highly selected for in the riparian areas where they were present in small clumps scattered widely over the gravel bars.

Although preference values indicate selection of food species, relative use of forage plants is also an important consideration. Species with extremely high PR values, such as some of the leguminous forbs, are not abundant and can not alone comprise the bulk of the muskox's diet. Plants such as willow may be more important due to their abundance and relatively high preference. Selection of nutritious forbs in association with willow contributes to the quality of the diet. A_x and G_x values, used in calculating the preference ratios, are listed in Appendix B. The relationship between these values more clearly illustrates the relative use of forage plants by muskoxen.

Fecal Sample Analysis

Ptarmigan fecal samples were collected in early May 1978 and showed a high percentage of willow (93.6 %) and Dryas integrifolia (6.2 %) as was the case for muskoxen at this time of year. Ptarmigan also took a small amount of Equisetum spp. (0.3 %). Caribou fecal samples were collected in mid-June 1979 and showed a high percentage of willow (87.9 %), Carex spp. (3.4 %), moss (2.9 %) and lichen (2.6 %). The remaining 3.2 % was made up of Vaccinium spp., Equisetum spp., Ledum spp., Astragalus spp., Cerastium spp., Peltigera spp., Saxifraga spp., unidentified legumes and unknown grasses.

A comparison of fecal analysis data with forage preference ratios shows some striking differences. Plants such as mosses and Carex spp., which may have high frequencies in the fecal samples, suggesting high preference, may nevertheless have relatively low measured preference ratios. Similarly, some plants observed eaten in large amounts do not occur in the fecal analyses in proportions expected (Appendix B). During mid-summer legumes are an important component of the muskox diet yet these plants appear in limited amounts or not at all in the fecal analyses results. An explanation for these discrepancies is that forage plants do not necessarily occur in fecal samples in the same proportions eaten. In addition, some species fragment more than others and are often over-represented in the analysis. Pulliam and Nelson (1979) have shown that fecal analyses are biased by the varying rates of digestion of food plants and they suggest that if fecal analysis is to yield accurate results differential digestion rates among forage species at their various phenological stages should be documented.

At Prudhoe Bay, White *et al.* (1975) investigated *in vitro* digestibilities for selected species using caribou and reindeer rumen liquor. Dry matter digestibilities for leaves and buds of willows (*Salix arctica*, *S. pulchra*=*planifolia*, *S. reticulata*, *S. ovalifolia*, and *S. lanata*) generally ranged from 34-54 % although one sample, when incubated with caribou liquor, received a high digestibility of 71 %. In contrast, forbs (*Oxytropis* leaves, the whole plant of *Parrya nudicaulis*, *Artemisia spp*. leaves, *Pedicularis* spp. infloresence and leaves) had high digestibilities ranging from 64-70 %. Mature leaves of *Eriophorum vaginatum* had a low digestibility of 20 %. Leaves of the grasses *Dupontia Fischeri* and *Arctophila fulva* had high digestibilities ranging from 56-79 %. Information on digestibilities of native plant species using rumen liquor from muskoxen would provide a more precise basis for understanding the relationship between fecal analyses and field observations of plants grazed in the present study. Experiments with captive muskoxen at the University of Alaska should provide such information in the future.

Regardless of the problems in interpreting fecal analyses, some characteristics of muskox forage use are apparent in the data presented. Table 2 shows the comparison of the relative densities of plant fragments of pooled fecal samples collected in late summer for three years. Most striking are the high frequencies of occurrence for willow (*Salix* spp.: 59.8, 76.7 and 95.8 %) which agree with my observations of high willow use by muskoxen in late summer. Grasses and sedges occurred in small amounts, also in agreement with my observations, with the exception of *Carex* spp. (16.7, 15.2 and 2.2 %). *Carex* spp. is quite abundant and may be more available than other graminoid species to foraging muskoxen. In relation to its abundance, however, *Carex* spp. is not an important item in the muskox diet. The value for late summer for *Astragalus* spp. for August 1977 is high (11.1 %) while the values for late summer 1978 and 1979 are quite low. *Astragalus* spp. is an important forage plant and its high digestibility may

Table 2. Between-year comparisons of identified plant fragments from pooled muskox fecal samples for three summers, Sadlerochit River, Alaska. Based on 100 fields per sample.

Species	Percent relative densities August 1977 n=13	July 1978 n=46	August 1979 n=64
Arctagrostis latifolia	1.6		
Astragalus spp.	11.1	1.4	0.9
Betula nana	0.4		
Bromus spp.	1.2		
Calamagrostis spp.	1.2		
Carex spp.	16.7	15.2	2.2
Cerastium spp.		0.5	
Deschampsia caespitosa	0.1		
Equisetum spp.	4.1	0.5	0.9
Eriophorum spp.	0.5	5.4	
Kobresia spp.	0.4		
Poa spp.	0.1	0.5	
Salix spp.	59.8	76.7	95.8
Stellaria spp.	0.1		
lichen	0.6		
moss	2.2		

explain why frequency values vary so much. Dwarf birch (Betula nana), a very common dwarf shrub in the non-riparian areas, appears once with a very low frequency (0.4 %). This species is quite resinous and is not often taken by muskoxen.

Table 3 presents adult/calf comparisons of fecal analyses in late spring and early summer. The calf sample from 31 May shows an unusually high frequency of use of moss (75.7 %) and an unusually low frequency of use of willow (4.3 %). In late May, however, calves are rarely more than two weeks old and may be experimenting with forage never before seen. Incidental ingestion of low-growing cryptogams is also likely just after snowmelt when new vegetation has not yet appeared. Moss has a very low digestibility in reindeer (Trudell et al. in press) and presumably muskoxen, and the young calf at this time would not likely have sufficient rumen development to allow efficient digestion of forage. These factors may be responsible for the unusually high moss frequency in the fecal material. A calf sample collected on 21 June shows a very high frequency of willow (91.1 %) and no value for moss, which is more comparable to the adult samples shown. Most calves are at least four weeks old by this time and are no doubt more experienced in foraging for food.

Table 3. Adult/calf comparisons of identified plant fragments from pooled muskox fecal samples for spring and summer, 1979, Sadlerochit River, Alaska. Based on 100 fields per sample.

	Percent relative densities			
	Calf		Adult	
Species	31 May n=1	21 June n=1	30 May n=1	19 June n=1
Carex spp.	16.9	0.4	21.1	13.6
Dryas integrifolia				0.4
Dupontia fischeri			0.8	
Eriphorum spp.				0.4
Salix spp.	4.3	91.1	68.7	84.5
Stellaria			0.4	
Vaccinium spp.	1.1			
lichen	2.1	3.9	2.0	3.5
moss	75.7		7.0	
mushroom				5.0

Taller, new vegetation masks low-growing cryptogams which may have been ingested earlier and the calves' rumens are probably sufficiently developed to digest green forage by this time. The values for the adult at 31 May show a high dependence on willow (68.7 %) and a rather high value for *Carex* spp. (21.1 %). By 21 June, however, occurrence of willow has increased (84.5 %) with a corresponding decrease in occurrence of *Carex* spp. (13.6 %).

The data presented in Table 4 show an interesting comparison among frequencies in the three major areas used by muskoxen in the ANWR: the Sadlerochit study area, the Tamayariak River drainage to the west and the Jago River drainage to the east. On the basis of the fecal analyses, willow use is high throughout the summer on the Sadlerochit drainage (Tables 2, 3 and 4). Willow is less abundant in the Tamayariak and Jago drainages and presence of willow in the feces is lower and sedges higher in these areas. This suggests that muskoxen are depending more on sedges and possibly forbs for their nutritive needs in areas where willow is not abundant. This is especially interesting because productivity of muskoxen in these areas has been lower than those of muskoxen in the Sadlerochit River drainage (Roseneau and Stern 1974, Bente 1977).

Table 4. Between-site comparisons of identified plant fragments from pooled muskox fecal samples, 1978, ANWR, Alaska. Based on 100 fields per sample.

	Percent relative densities			
	Sadlerochit R.		Tamayariak R.	Jago R.
Species	July 2-11 n=46	July 15-27 n=46	August 15, 17 n=2	August 22 n=1
Astragalus spp.		1.4		1.1
Carex spp.	17.5	15.2	63.7	23.3
Cerastium spp.		0.5		
Dryas integrifolia	0.6			0.4
Dupontia fischeri	0.6		0.4	
Equisetum spp.	6.1	0.5		7.1
Eriophorum spp.	4.2	5.4	2.7	
Festuca spp.				0.4
Luzula spp.				0.4
Poa spp.		0.5		
Salix spp.	68.0	76.7	32.7	67.5
Saxifraga spp.	1.2			
Stellaria longipes	1.2		0.4	

Results of muskox fecal analyses from the Seward Peninsula, Alaska and from Sondre Stromfjord, West Greenland are presented for comparison with the Sadlerochit study area in Table 5. On the Seward Peninsula, the calf diet is comparable with that of the yearling and adult. Small amounts of grasses (0.4 and 0.7 %), dwarf shrubs (0.4 and 0.4 %) and moss (0.4 %) do occur in the calf's feces, perhaps for the same reasons mentioned previously. The analysis of winter fecal pellets collected from an adult muskox shows moderately high use of willow although less than during summer. The frequency of use of cryptogams (7.5 and 8.9 %) and _Empetrum nigrum_ (5.8 %) is important to note as these plants are also used on Nunivak Island at this time of year (Bos 1967).

Species composition of muskox fecal samples from West Greenland is dramatically different from those in the Alaskan samples. Willow is not abundant in Greenland (H. Thing pers. comm.) but grasses and sedges are. According to this sample, forbs such as _Cerastium_ spp. (18.7 %) and _Potentilla_ spp. (10.8 %) are more important than in the Alaskan samples and _Salix_ spp. occurs in a much lower percentage (6.0 %). Grasses such as _Festuca_ spp. (24.5 %) and _Poa_ spp. (3.7 %) are quite important to muskoxen. Other grasses (13.0 %) also comprise a large part of the

Table 5. Between-site comparisons of identified plant fragments from muskox fecal samples collected from calf, yearling, and adult animals at two Alaskan sites and Sarfartoq Valley, W. Greenland. The Sadlerochit sample was collected from the entire herd. Seward Peninsula samples were collected by D. R. Klein and those from West Greenland by D. Roby.

	Percent relative densities					
	Sadlerochit R.	Seward Peninsula				West Greenland
	3,4 May 1978	June 28 1979				25 May 1978
		calf	yearling	adult		adult
				fresh	winter	
Species	n=46	n=1	n=1	n=1	n=1	n=1
Agrostis spp.				0.1		0.7
Carex spp.	1.3	4.4	4.0	4.5	5.8	10.8
Cerastium spp.						18.7
Deschampsia (type)						0.7
Dryas spp.	2.6	0.4				6.0
Dupontia fischeri	0.4					
Empetrum nigrum					5.8	
Equisetum spp.		1.4	0.4			0.7
Festuca (type)	0.8	0.4		0.2		24.5
Poa (type)	0.4					3.7
Potentilla (type)						10.8
Rubus spp.		0.4				
Salix spp.	92.0	92.1	95.5	95.0	70.8	6.0
Saxifraga spp.	0.8					
Stellaria longipes	0.8					
lichen					7.5	
moss	0.8	0.4	0.1	0.3	8.9	
unident. forb						0.7
unident. grass		0.7			0.6	11.6
unident. legume						5.2
unident. seed						0.6

diet as reflected in the fecal samples.

Muskox Food Habits

Some inferences can be made on the important plant species and the seasonal changes in the diet of the muskoxen on the Sadlerochit River.

In late winter, the animals were observed browsing primarily on twigs of *Salix alaxensis*, *S. planifolia* and *S. lanata* and on old leaves and stems of *Lupinus arcticus* and *Dryas integrifolia*. Feeding site analysis revealed that in late May muskoxen fed on the young flowering heads of *Eriophorum vaginatum*, which is one of the first plant species in the Arctic to break dormancy. Later the new leaves of *E. vaginatum* and new growth of *Carex bigelowii* were taken. By mid-June muskoxen supplemented their diet with and fed more intensively on the new leaves of *Salix planifolia*, which was a common species in the tussock meadows. Feeding animals commonly jerked their heads up and down as they stripped leaves from willow twigs. As other plants initiated growth the muskoxen spent more time in the riparian areas, included more willow (*Salix alaxensis*) in their diet and fed on forbs. These forbs included: *Epilobium latifolium*, *Oxytropis maydelliana*, Hedysarum mackenzii, Astragalus alpinus, Castilleja caudata and Pedicularis verticillata. Some of these plants, as well as Pedicularis kanei, Petasites frigidus and Polygonum bistorta, also grew in the more upland areas and the new leaves and flowers of these species were grazed when the muskoxen were in these areas in early July. When willow twigs were young, muskoxen often clipped off the new growth along with the leaves but as the summer progressed into July and secondary tissue was laid down, leaves were stripped without removing much of the new, woody growth. By late summer (mid-August) willow leaves were the primary forage consumed but muskoxen were supplementing their diet with some forb leaves and the seed capsules of Oxytropis maydelliana, Astragalus alpinus and Hedysarum mackenzii. In late October muskoxen were observed foraging through the snow on the dried leaves and senescent twigs of Salix alaxensis, S. planifolia, the dried leaves and stems of Astragalus spp., Artemisia spp. and Stellaria longipes, the green stems of Equisetum variegatum, the dried leaves of Oxyria digyna and the green basal parts of Lupinus arcticus and Oxytropis maydelliana, which include the overwintering buds (K.T. Jingfors pers. comm.).

Other authors have documented muskox food habits for Alaska, Canada, Greenland and Scandinavia, as shown in

Table 6. On Nunivak Island, Bos (1967) found muskoxen eating *Salix planifolia* in the summer as they did on the Sadlerochit River (stripping leaves from twigs). *Salix alaxensis* was also used but because of its limited distribution it was less important. Muskoxen also ate *Carex aquatilis*, *Calamagrostis canadensis* and associated graminoids, plants considered to be unimportant to the Sadlerochit muskoxen. Winter range is limited on the island and is restricted to its outer perimeter where winds sweep the vegetation relatively free of snow. Here *Elymus mollis* (=*arenarius*) and *Empetrum nigrum* were fed upon most heavily. Other species were present in the diet and the reader is referred to Bos' work for more information. Spencer and Lensink (1970) also found *E. mollis* to be important on Nunivak Island during winter. They listed sedges (*Carex* spp.), *Empetrum nigrum*, and *Ledum palustre* as important winter forage species. Although these species were common in the Sadlerochit River study area, muskoxen avoided them and depended more on *Salix* spp. and forbs during winter. In the winter of 1970 Lent and Knutson (1971) found muskoxen on Nunivak feeding on *Elymus mollis*, *Carex* spp. and *Luzula* spp.

A group of muskoxen, transplanted to the Seward Peninsula in 1969, were observed near California River in

Table 6. Summary of primary food species used by muskoxen in Alaska, Canada, Greenland and Scandinavia.

Location	Author	Summer	Winter
Alaska			
Nunivak Island	Bos (1967)	*Salix planifolia* *Carex aquatilis* *Calamagrostis canadensis*	*Elymus mollis* (=*arenarius*) *Empetrum nigrum*
•	Spencer and Lensink (1970)	———	*Elymus mollis* *Ledum palustre* *Empetrum nigrum*
•	Lent and Knutson (1971)	———	*Elymus mollis* *Carex* spp. *Luzula* spp.
Seward Peninsula	Jingfors (pers. comm.)	*Salix lanata* *S. glauca* *Angelica lucida*	———
Sadlerochit River	this study	*Salix alaxensis* *Oxytropis maydelliana* *Astragalus alpinus*	*Salix alaxensis* *S. planifolia* *Lupinus arcticus*
Canada			
Thelon Game Sanctuary	Tener (1965)	*Salix alaxensis* *Carex stans*	*Ledum decumbens* *Empetrum nigrum* *Vaccinium vitis-idaea*
Fosheim Peninsula, Ellesmere Island	•	*Poa* spp. *Puccinellia angustata* *Festuca brachyphylla*	*Salix* spp. *Dryas integrifolia*
Lake Hazen, Ellesmere Island		*Salix arctica* *Oxyria digyna* *Epilobium latifolium*	dried grasses and sedges
Devon Island	Hubert (1974)	grasses and sedges *Salix* spp.	———
Banks Island	Wilkinson *et al.* (1976)	*Carex stans*	———
Bailey Point, Melville Island Mokka Fiord, Axel Heiberg Island Bracebridge Inlet, Bathurst Island Devon Island Ellesmere Island	Parker (1978)	sedges *Salix* spp.	sedges
Polar Bear Pass, Bathurst Is.	Jingfors (pers. comm.)	*Carex stans* *Salix arctica*	———

Table 6. (cont.)

Location	Author	Summer	Winter
Greenland			
East Greenland	Ferns (1977)	*Salix arctica*	———
Sarfartoq Valley, West Greenland	Roby (1978 a)	*Trisetum spicatum* *Festuca brachyphylla* *Poa glauca*	sedges *Salix glauca*
Scandinavia			
Spitzbergen, Norway	Alendal (1974)	*Alopecurus alpinus* *Poa alpigena* *Festuca* spp. sedges *Oxyria digyna*	———
Sweden	Jingfors (pers. comm.)	*Salix* spp. forbs *Pinus sylvestris*	———

summer 1979 feeding on plant species similar to those used by muskoxen on the Sadlerochit River (D.R. Klein pers. comm.). In June and July 1980 Jingfors (pers. comm.) observed the same herd of muskoxen feeding on new leaves of *Salix lanata* and *S. glauca* in willow thickets along creeks in the vicinity of Black Mountain 20 km northwest of Brevig Mission. These muskoxen were grazing species which did not occur in the Sadlerochit River drainage, such as *Angelica lucida*, *Iris setosa*, *Sedum rosea*, *Allium schoenoprasum*, as well as *Artemisia arctica*, which did occur along the Sadlerochit River and which was also grazed by muskoxen during the present study.

Tener (1965) found muskoxen feeding primarily on *Salix alaxensis* in the summer in the Thelon Game Sanctuary, Northwest Territories, as they did along the Sadlerochit River. *Carex stans*, *C. capitata*, *Juncus castaneus*, *Poa alpina* and *Equisetum arvense* were also taken. Although these plants did occur in the Sadlerochit drainage, muskoxen rarely fed on them. Tener also gave information on summer muskox food habits on the Fosheim Peninsula, Ellesmere Island. There, grasses (*Poa* spp., *Puccinellia angustata* and *Festuca brachyphylla*) were important and willows (*Salix* spp.) were eaten only occassionally. At times, marshy vegetation (*Dupontia fischeri* and *Deschampsia* brevifolia) was consumed. At Lake Hazen on Ellesmere Island, the rumen contents of three bulls examined by Tener consisted of grasses (Alopecurus spp. and Festuca spp.), willow (Salix arctica), some sedge (Carex stans) and some Dryas integrifolia. During summer, animals were observed eating Oxyria digyna, Carex nardina, C. stans, Poa glauca and new willow leaves and twigs. Evidence of heavy willow browsing was apparent. Animals were also selecting Epilobium latifolium, a species often selected by the Sadlerochit muskoxen, and Melandrium trifolium. In the Thelon Game Sanctuary, woody species were of more importance in winter. Ledum decumbens, Empetrum nigrum, Vaccinium vitis-idaea, V. uliginosum, and Betula nana were taken. On Ellesmere Island, muskoxen depended more on willow, Dryas integrifolia, dried grasses and sedges since the woody species previously mentioned did not occur in the High Arctic.

Parker (1978) collected muskox rumen and fecal samples from various locations in the Canadian High Arctic (Bailey Point, Melville Island; Mokka Fiord, Axel Heiberg Island; Bracebridge Inlet, Bathurst Island; Devon Island and Ellesmere Island). From plant fragmentation analysis he stated that muskoxen prefer a sedge-willow diet in the summer and a sedge diet in the winter. He claimed that muskoxen maintain better condition over the winter when on a sedge diet, but under severe winter conditions they may be forced to seek out willow, grasses and forbs on exposed slopes. This does not agree with what was observed on the Sadlerochit River where muskoxen were depending primarily on willow and forbs in the winter, and where survival rates and calving success the following spring were very high (Jingfors 1980).

Jingfors observed muskoxen at Polar Bear Pass, Bathurst Island, feeding on *Carex stans*, *Salix arctica* and *Saxifraga oppositifolia* during the summer of 1978 (K.T. Jingfors pers. comm.). Hubert (1974) found muskoxen feeding predominantly on monocot vegetation with some ingestion of *Salix* spp. on Devon Island. Likewise, Wilkinson *et al*. (1976) found muskoxen on north central Banks Island foraging mostly in wet habitats and feeding almost exclusively on lush sedges (*Carex stans*) with some use of grasses and willows. The work of Wilkinson *et al*. involved the visual inspection of plots and analysis of rumen samples. The differences in forage preferences of muskoxen between the Thelon Game Sanctuary, which is located on the Canadian mainland, and the Alaskan Arctic and the other arctic islands is apparently explained by the availability of forage. Banks Island offers very little willow but has abundant sedge growth, while willows are much more common in the Thelon Game Sanctuary and in arctic Alaska, and they appear to be more important to muskoxen in these areas.

In East Greenland, Ferns (1977) found muskoxen feeding on Salix arctica in dry stream beds in July, although willow is not as abundant in Greenland as in the Alaskan Arctic. Roby (1978 b) noted that, during winter, introduced muskoxen in the Sarfartoq Valley of western Greenland fed on sedges in wet meadows and on willows (Salix glauca) growing on south-facing slopes. In late spring they were feeding primarily on steep, south-facing slopes and eating Trisetum spicatum, Festuca brachyphylla and Poa glauca. This valley is the site of unique growths of tall willow (S. glauca) that the muskoxen also feed and rub upon. Roby noted that these thickets were decreasing in area because of heavy use by muskoxen. In some summers the muskoxen leave the area, apparently because of harassment by aircraft and other human disturbance.

On Nordenskiold Land, Spitzbergen, in the Svalbard Archipelago, Alendal (1974) found muskoxen introduced to the area feeding on Alopecurus alpinus, Poa alpigena, Festuca spp., sedges and Oxyria digyna during the summer months. *Salix arctica*, preferred in other areas, is not found in Svalbard although *S. polaris* does grow here. Reindeer are native to this area and Alendal suggests that they may have been effectively competing with muskoxen for food. The muskox population has declined rapidly in recent years, coinciding with an increase in reindeer numbers, and only three individuals remained in 1980 (H. Staaland pers. comm.).

Muskoxen have established in Sweden from an introduced population in Norway and evidence of browsing on pine (*Pinus sylvestris*) was noted there in September 1979 (K.T. Jingfors pers. comm.) This was probably a rare occurrence, since grazing on willow and forbs, as along the Sadlerochit River, was also evident and more widespread.

In summary, willow was used as a major food source by the Sadlerochit muskoxen. In mid- and late summer it was heavily used. Forbs, especially legumes, were highly selected for during summer, although they were not as abundant as willow. Grasses and sedges were little used in relation to their abundance, although *Eriophorum vaginatum* was selected for in late May. Food habits of muskoxen from other areas in northern Alaska and mainland Canada and Scandinavia show similar high use of willow. Muskoxen in the Canadian High Arctic, however depend more on sedges and those in Greenland and Spitzbergen have a heavier dependency on grasses.

III. RANGE PRODUCTIVITY

Annual plant growth rates in the Arctic are low as compared with those in more temperate ecosystems. However, daily growth rates during the short, cool growing seasons are much more comparable to and may even exceed growth rates in more temperate ecosystems (Billings and Mooney 1968). Temperature, wind exposure, solar radiation, snow cover, moisture, availability of soil nutrients and successional processes all affect the rate of primary production (Bliss 1971). Tundra plants may be exposed to air temperatures less than -10 C to nearly 40 C during the growing season, and net positive photosynthesis often continues at temperatures below 0 C, as long as the leaves are not frozen and other conditions are favorable (Wielgolaski 1980).

Schultz (1964) and Ulrich and Gersper (1978) have shown that low growth rates in the Arctic may be due to a deficiency of available nutrients in the soil. Many of the minerals necessary for plant growth, such as nitrogen, phosphorus and potassium, are present but are inaccessible in the frozen ground for much of the growing season. These nutrients may be released slowly because of the cool soils which slow chemical processes. Microorganism activity which might promote release of important nutrients is inhibited by the low temperatures, and therefore dead plant material accumulates. Lush plant growth is noticeable around naturally fertilized areas such as raised hummocks used as bird perches, animal carcasses and drainage channels. Tundra soils that have been fertilized with inorganic nutrients have responded with dramatic increases in plant growth (Schultz 1964, McKendrick et al. 1978). Standing dead plant biomass accumulates with time in wet sites in the Arctic. When plant material is removed by grazing or clipping, in such sites, more solar radiation is able to penetrate the ground and the active thaw layer increases. Mineral nutrients then become more available to plants which respond with an increase in growth. Grazing, therefore, can play an important part in facilitating the recycling of nutrients in the tundra ecosystem.

Biomass Productivity

Above-ground current season's production ($g \cdot m^{-2}$) for eight potential forage species sampled throughout the growing season is presented in Figure 8. Production at the height of the season (22 July) differed significantly between species ($p<0.05$). This indicates that certain species within the areas tested produce more green material per unit area during the growing season than others.

In all cases, after an initial increase in biomass production there was a lag in late June. On 23 June 1979 the weather became unseasonally cold and 100 mm of snow accumulated. This probably explains why a dramatic increase in growth did not occur for most species until early July. Maximum biomass was achieved in early August. Plants began senescence in mid-August and the above-ground parts of most species rapidly lost weight after this time. By 1 September current season's growth had decreased dramatically in weight, mainly due to leaf abscission.

The production exhibited by the willow _Salix alaxensis_, a preferred muskox forage species, was of the greatest magnitude and peaked at 82.4 $g \cdot m^{-2}$ on 11 August. _S. planifolia_, from a mesic site, exhibited similar growth and peaked at 79.3 $g \cdot m^{-2}$ on 11 August but peak growth for the same species in a drier site was much less (11.4 $g \cdot m^{-2}$). Muskoxen fed on this species in both dry and moist areas in June when the differences in growth between the

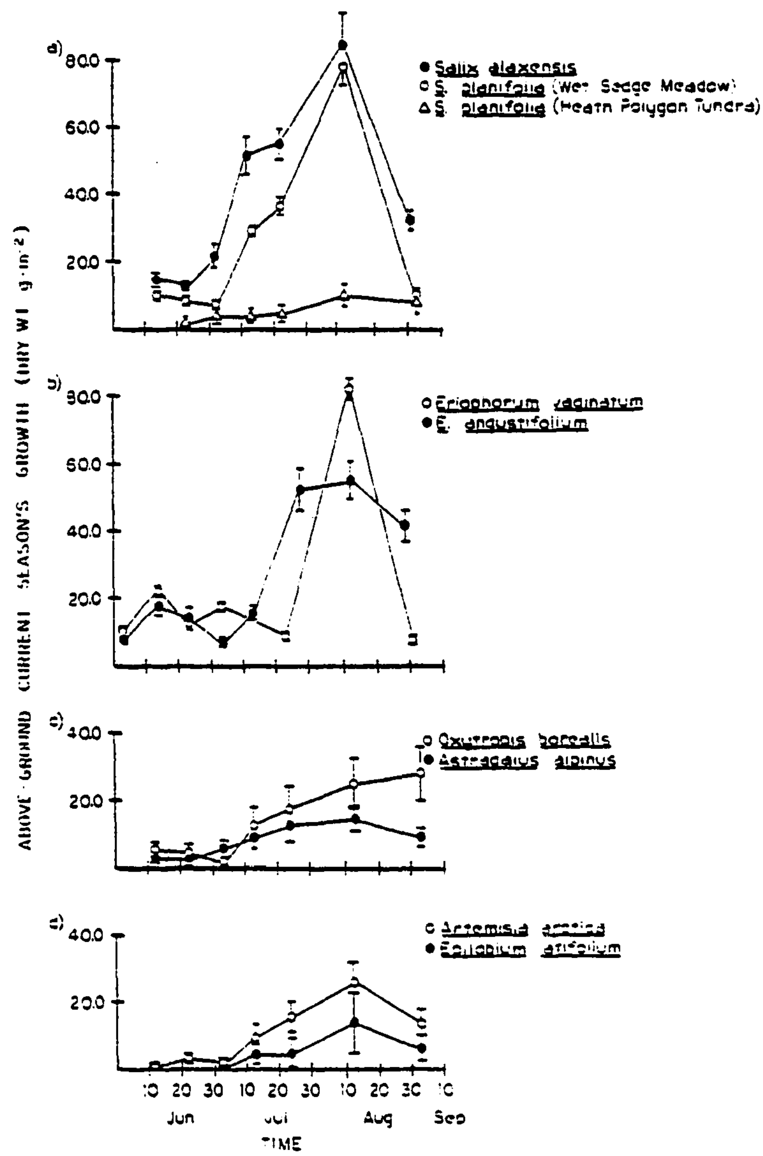


Figure 8. Seasonal trend in above-ground current season's production, summer, 1979, for: a) two willow species, b) two sedge species, c) two leguminous forbs and d) two other forbs. (x, s.d., n=30).

two sites were not great. Later in the summer, when the S. planifolia which grew in wet sites became lush, muskoxen spent more time in the riparian drainages feeding on forbs and S. alaxensis. However, in October and March Jingfors (pers. comm.) noted that muskoxen were feeding heavily on S. planifolia in small drainages and gullies.

The growth of the two species of Eriophorum was erratic, perhaps because of different moisture regimes within the two sites, but they still peaked in late summer. The four forb species had similar growth patterns which may be due to their similar growth forms and Riparian Habitat preferences. Of the four, Oxytropis borealis had the greatest current season's above-ground growth (23.3 g$\cdot$m^{-2}) at 11 August. Unlike the other forbs it did not decline in biomass but actually increased to 24.6 g$\cdot$m^{-2} on 1 September. The stems and leaves of this species are covered with small glands which exude a sticky, aromatic substance. Although it was occasionally fed upon (PR=0.1), muskoxen did not feed on this species as heavily as on the other leguminous forbs.

Tener (1965) measured dry weight production of important species at the Thelon Game Sanctuary, Canada (Table 7). Of special interest is Tener's dry weight

Table 7. Dry weight, above-ground production of selected muskox food species, Thelon Game Sanctuary, N.W.T., Canada. All data were gathered during the growing season. From Tener (1965).

	Annual production ($g \cdot m^{-2}$)		
	Summer range	Winter range	
Species		1	2
Salix richardsonii(=*lanata*)	6.3		
S. alaxensis	85.6		
S. arbusculoides	4.1		
Betula glandulosa		6.5	8.4
Empetrum nigrum		20.1	46.3
Ledum decumbens		22.6	35.0
Andromeda polifolia		6.3	
Vaccinium uliginosum		1.0	3.8
V. vitis-idaea		10.1	20.8

above-ground production of Salix alaxensis (85.6 g$\cdot$m^{-2}) from summer range. This is remarkably similar to production for the same species in the Sadlerochit River area (85.2 g$\cdot$m^{-2}). The abundance of this species may explain why muskoxen feed heavily on it at these locations. Empetrum nigrum, Ledum decumbens, and Vaccinium vitis-idaea, collected on winter range during the growing season, also exhibit high productivity. These species are all preferred winter forage species in the Thelon Game Sanctuary but we found little evidence that muskoxen ever fed heavily on these species in the Sadlerochit River study area. However, Bos (1967) notes that E. nigrum is used by muskoxen in the winter on Nunivak Island. Spencer and Lensink (1970) also noted the importance of E. nigrum on Nunivak Island as well as that of L. palustre. E. nigrum occurred in a winter fecal sample collected on the Seward Peninsula (Table 5), where it may be an important muskox winter forage species. Jingfors (1980) reported that willow production at Bathurst Island in the Canadian High Arctic was low (peak biomass value for the current year's growth for Salix arctica was 18.6 g$\cdot$m^{-2}) and the productivity of muskoxen in the same area was also low, as judged by the number of calves per cow. Willow production in the Sadlerochit River area was much higher as was the ratio of muskox calves per cow.

Nutrient Analysis

Comparative nitrogen values for 16 plant species are shown in Figures 9 and 10. Figure 9a presents values for four shrubs. After a build-up during June, nitrogen content for *Salix lanata* (3.56 %) and *S. planifolia* (3.14 %) peaked in early July and then dropped during the rest of the growing season (Figure 9a). *Betula nana* (2.95 %) did not peak until mid-July and never reached the high values of the preferred willow muskox forage.

The graminoid species (Figure 9b) showed a moderately high but irregular pattern for seasonal nitrogen content. Nitrogen content peaked in mid-July for *Carex aquatilis* (2.07 %), *Hierochloe alpina*, (2.50 %) and for *Eriophorum vaginatum* (1.92 %) which was later than for the willows. *E. vaginatum* however, also showed a very high nitrogen value for late May (2.14 %). This is important to note, for muskoxen were feeding heavily on the new flowers and leaves of this species during this short period of time. High nutrient content for *E. vaginatum* during snow-melt has been noted before (Chapin *et al*. 1980) and this species is also heavily fed on by caribou at this time (Kuropat and Bryant in press).

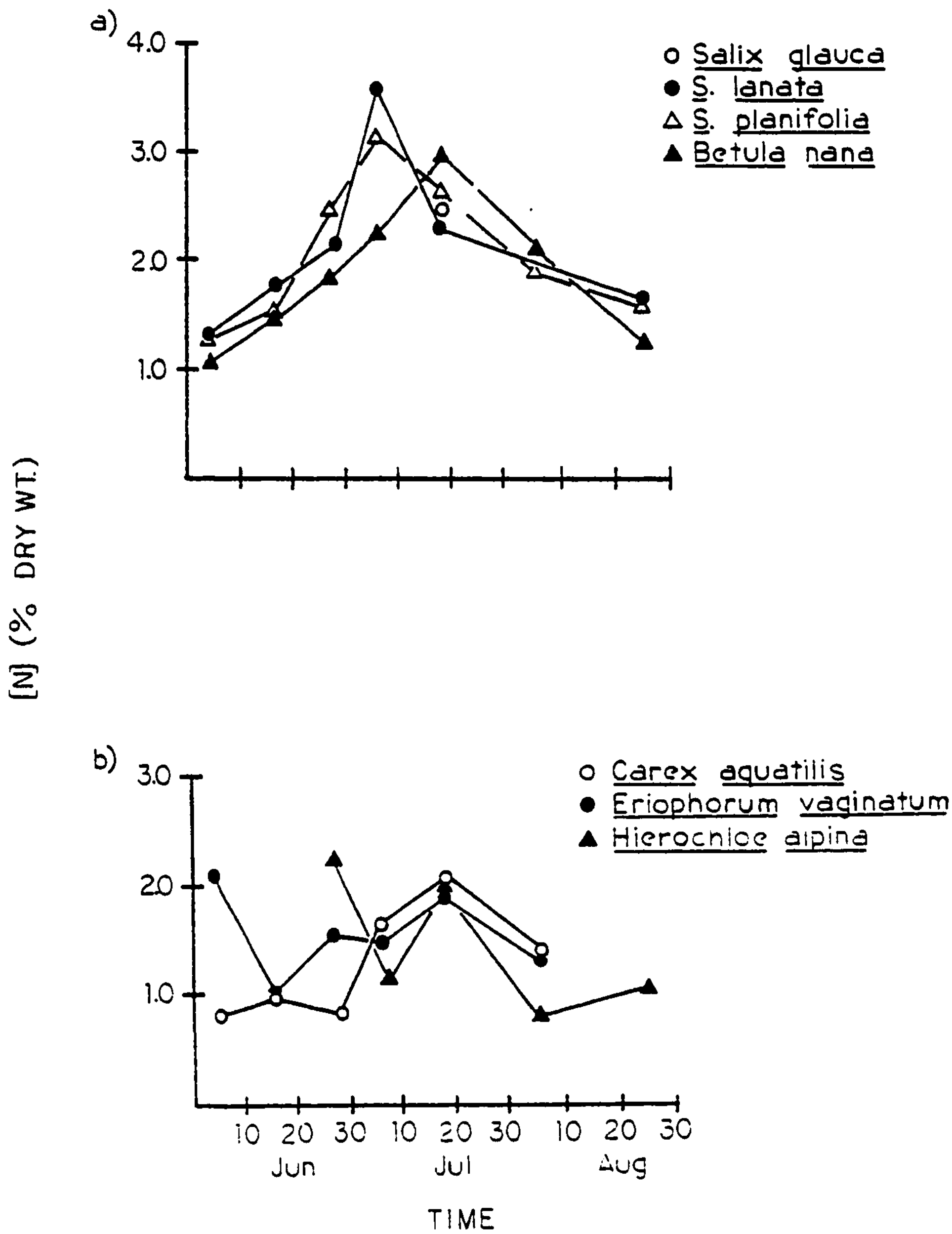


Figure 9. Seasonal nitrogen content of current season's production for: a) four woody species and b) three graminoid species.

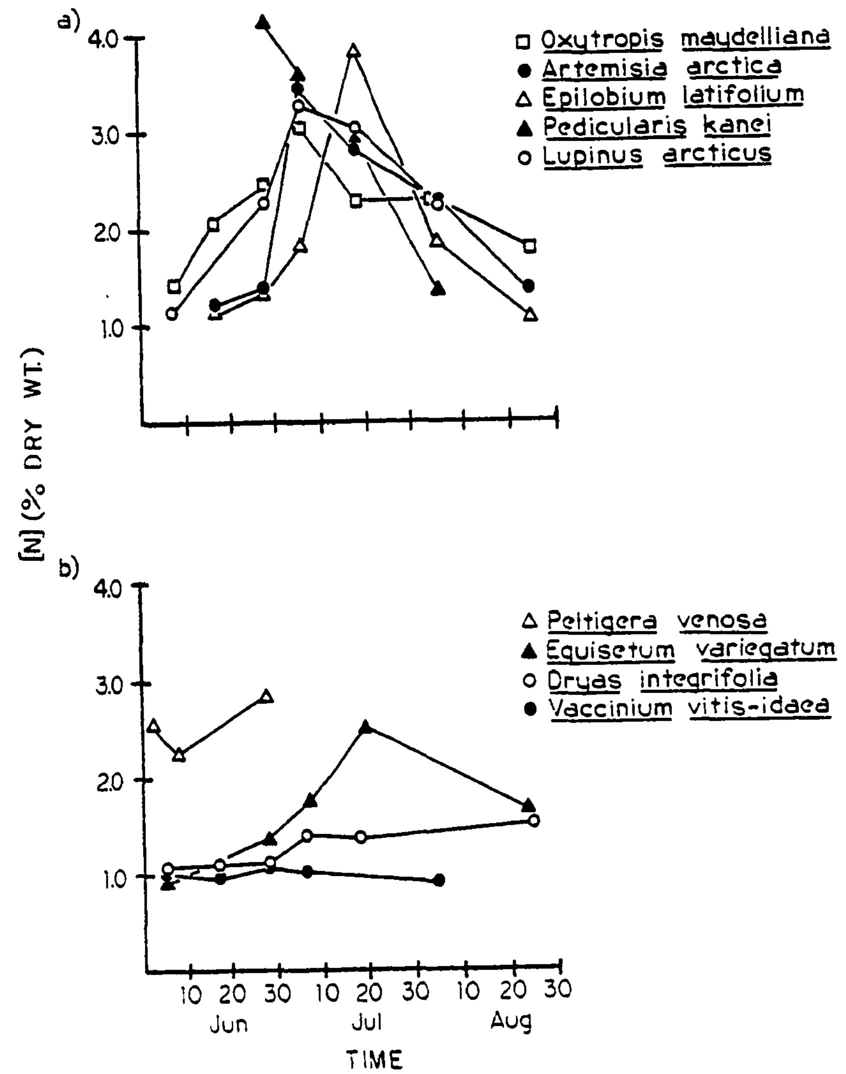


Figure 10. Seasonal nitrogen content of current season's production for: a) five forb species and b) two mat-forming species (Dryas integrifolia and Vaccinium vitis-idaea), a lichen (Peltigera venosa) and a horsetail (Equisetum variegatum).

Nitrogen content increased sharply during late June and peaked during early July for Artemisia arctica (3.48 %), Lupinus arcticus (3.28 %) and Oxytropis maydelliana (3.07 %), then declined rapidly during the growing season (Figure 10a). When nitrogen values were high, muskoxen often fed on the flowers and young leaves of these species. Pedicularis kanei had very high nitrogen levels early in the season (4.16 %) which later declined rapidly. This species initiates growth earlier than the other forbs, which may explain the early peak in its seasonal nitrogen distribution. Muskoxen were observed feeding on this species in late May and caribou were also seen feeding on it regularly. Epilobium latifolium, which initiated growth later than the forbs previously mentioned, usually blooms later and peaked in nitrogen content in mid-July (3.87 %).

The two mat-forming species, Dryas integrifolia and Vaccinium vitis-idaea, exhibited low nitrogen content throughout the season (Figure 10b). These are evergreen species and addition of new growth occurs at a low rate continuously throughout the growing season, which probably accounts for the low nutrient concentration. These species were not important to the Sadlerochit muskoxen. The horsetail, Equisetum variegatum, had a moderately high peak in mid-July (2.54 %), and muskoxen occasionally fed on it.

The foliose lichen Peltigera venosa showed high values for nitrogen content early in the spring when the ground was moist and most of its seasonal growth takes place. Cratering by muskoxen for P. venosa was evident in May before and during snow-melt.

Phosphorus concentration was much lower than nitrogen for all species and showed much less fluctuation during the growing season (Figure 11). Phosphorus content for all species peaked during mid-July and although of lower magnitude, distributions for Eriophorum vaginatum, Hierochloe alpina, Pedicularis kanei and Equisetum variegatum tracked their corresponding distributions for nitrogen. As with nitrogen content, phosphorus concentrations of E. vaginatum were high when muskoxen were eating it. Although peak biomass production was much later, muskoxen fed heavily on this species only early in the season when the nutrient value of E. vaginatum was high.

Calcium content for seven species is shown in Figure 12. Highest peak calcium concentrations were exhibited by the three forbs Epilobium latifolium (3.76 %), Artemisia arctica (3.07 %) and Pedicularis kanei (1.95 %). Salix lanata (1.36 %) and S. planifolia (0.61 %) had moderately

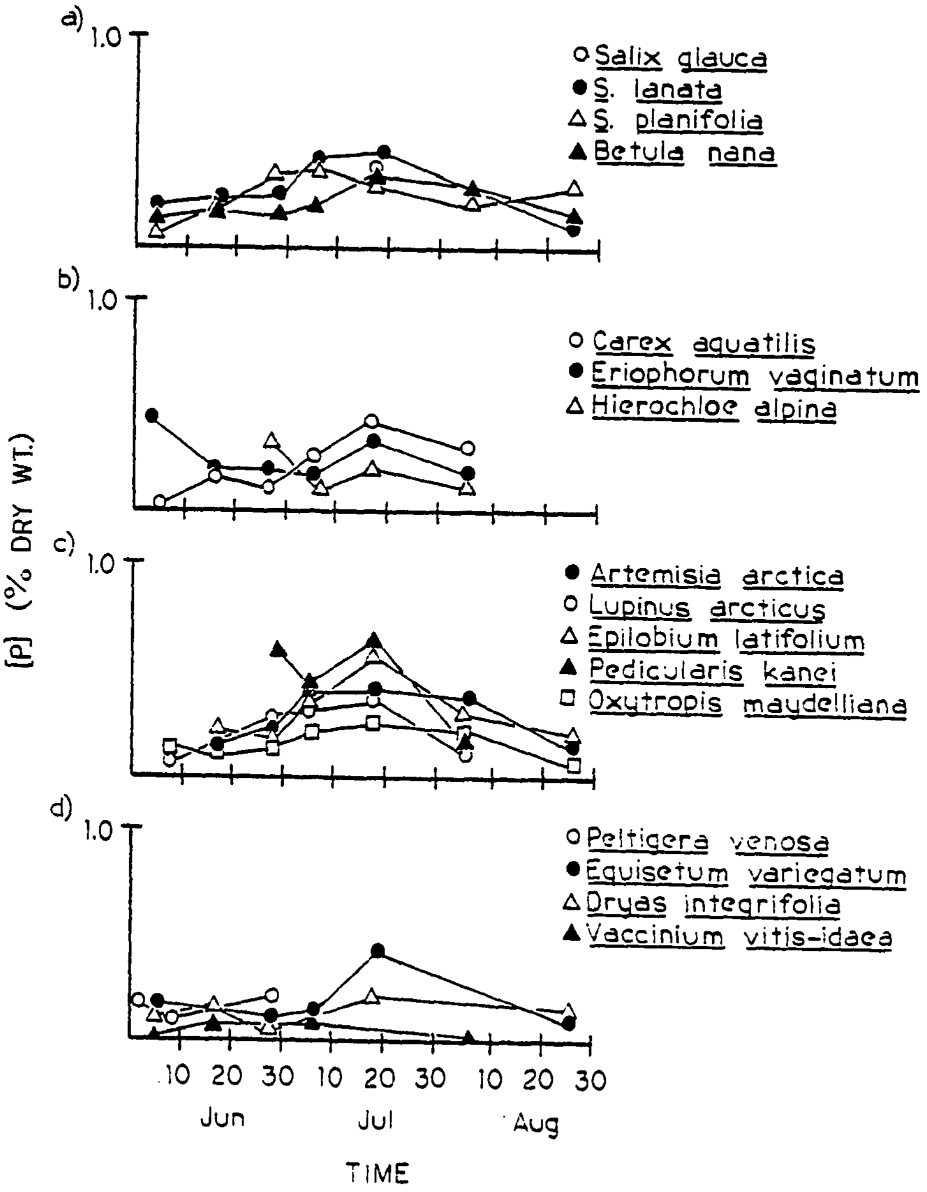


Figure 11. Seasonal phosphorus content of current season's production for: a) four woody species, b) three graminoid species, c)five forb species and d) two mat-forming species (*Dryas integrifolia* and *Vaccinium vitis-idaea*), a lichen (*Peltigera venosa*) and a horsetail (*Equisetum variegatum*).

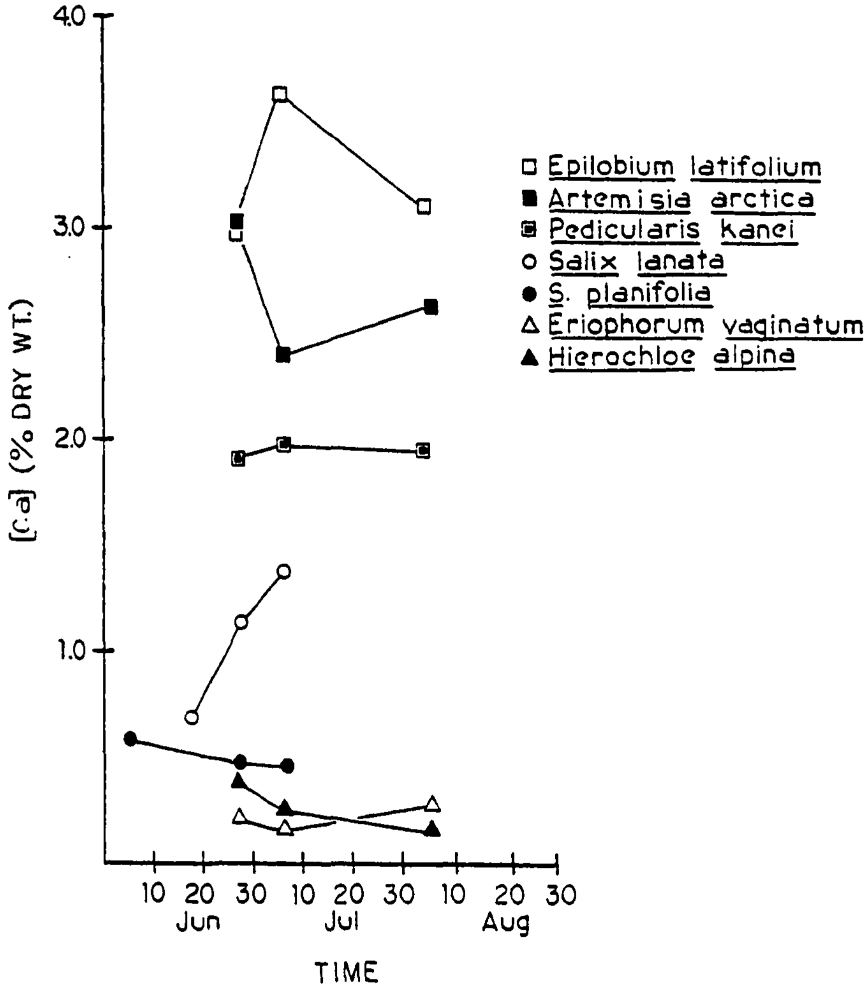


Figure 12. Seasonal calcium content of current season's production for seven plant species.

high peak calcium concentrations. The graminoids *Eriophorum vaginatum* (0.20 %) and *Hierochloe alpina* (0.34 %) had very low calcium concentrations.

The relationship between nutrient and biomass productivity for three important forage species is presented in Figures 13-15. For most species nitrogen content peaked early in the season and above-ground growth peaked in late July. Figures 13c, 14c and 15c show standing crop of nitrogen for *Salix planifolia*, *Epilobium latifolium* and *Artemisia arctica*. The different distributions produce a graph with two peaks for *S. planifolia* and *E. latifolium* and a graph for *A. arctica* with a broad, high distribution. High nutrient quality early in the growing season and a delayed peak biomass distribution provide muskoxen with a high quality diet throughout the growing season. Early in June when nitrogen and phosphorus concentrations were increasing, high quality forage was available to foraging muskoxen. Later in the season, although some forage decreased in nutritional value, the large biomass of food species available allowed muskoxen to improve the quality of their diet through increased food intake.

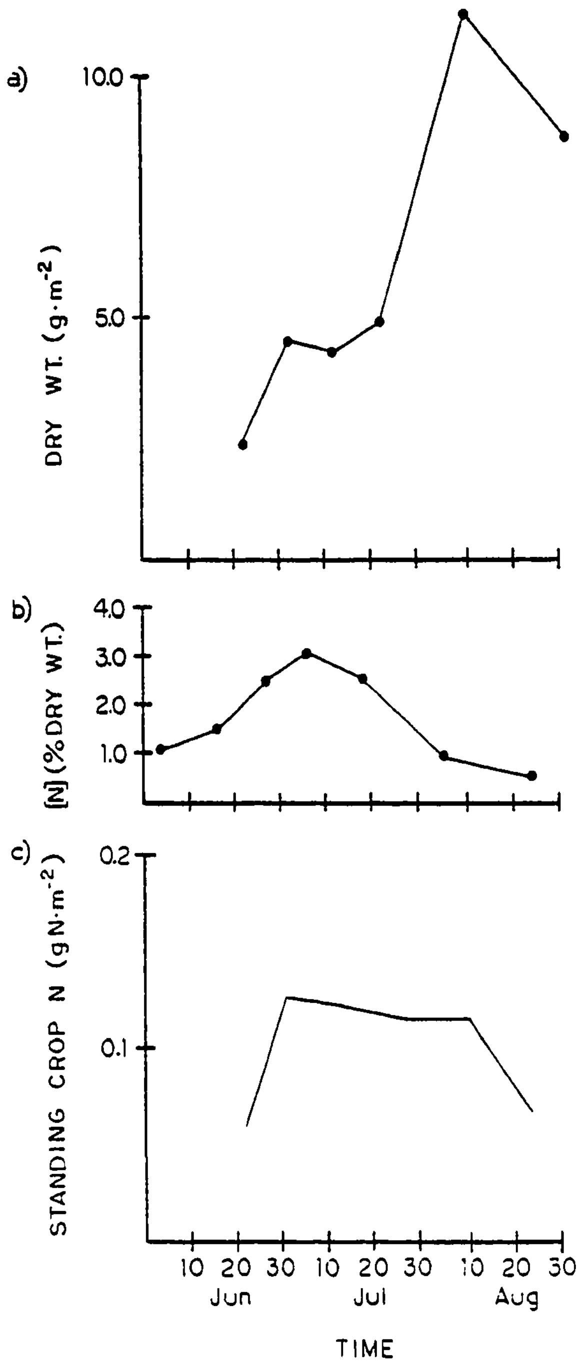


Figure 13. Productivity data for Salix planifolia: a) seasonal nitrogen content, b) seasonal trend of current season's above-ground growth and c) standing crop of nitrogen.

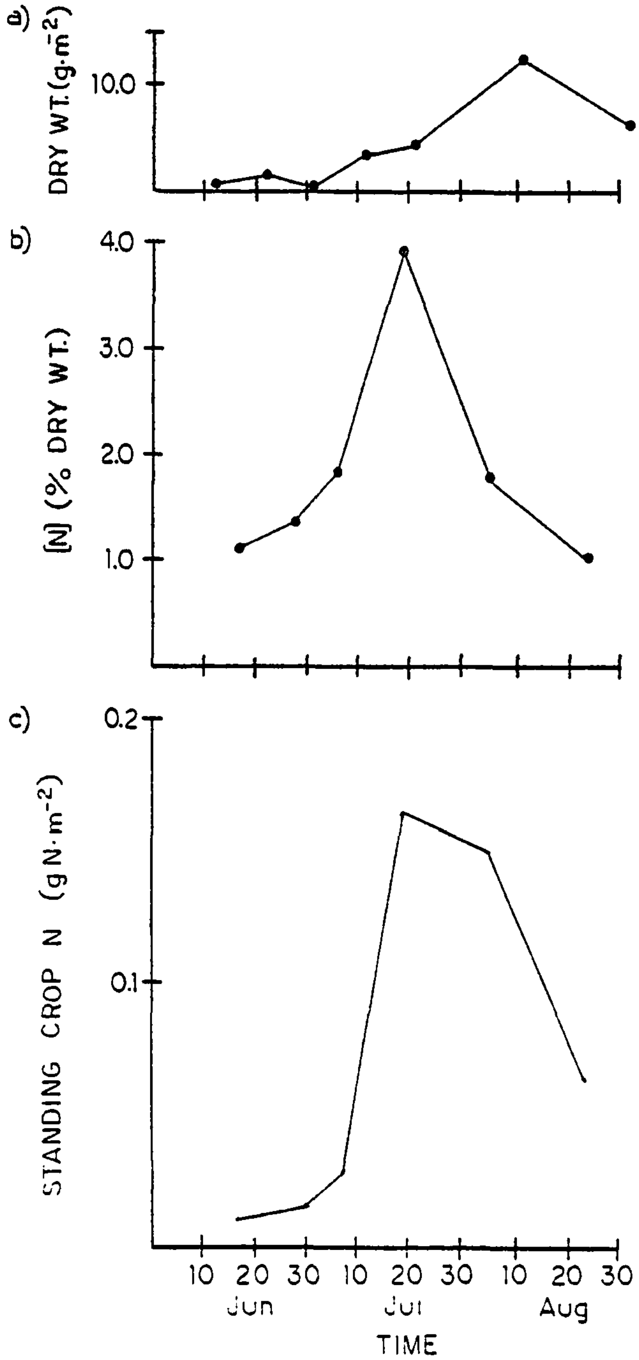


Figure 14. Productivity data for *Epilobium latifolium*: a) seasonal nitrogen content, b) seasonal trend of current season's above-ground growth and c) standing crop of nitrogen.

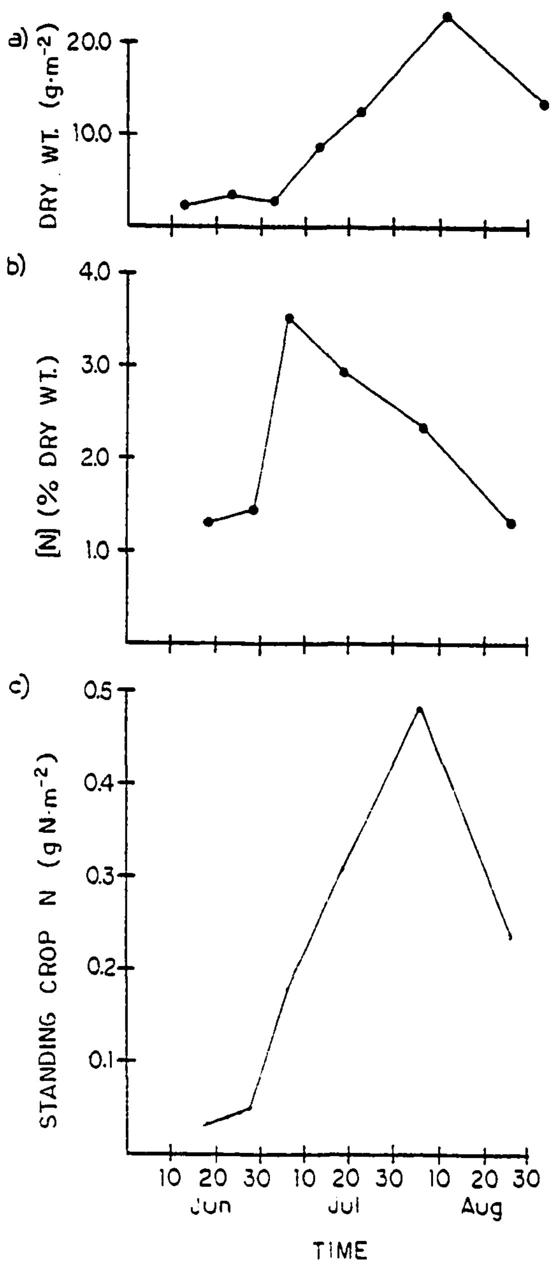


Figure 15. Productivity data for *Artemisia arctica*: a) seasonal nitrogen content, b) seasonal trend of current season's above-ground growth and c) standing crop of nitrogen.

Vegetative Diversity

Species richness of vascular plants collected in the area of the Sadlerochit base camp was examined and is listed in Table 8. Species collected at Prudhoe Bay and Barrow (Murray and Murray 1978) and at Nunivak Island (Bos 1967) are grouped similarly and are also listed as a basis for comparison. The Sadlerochit range included a slightly greater number of forb and shrub species as compared to these other areas. This may be a reflection of the more continental climate in the Sadlerochit area which has warmer summers than the other locations which are coastally influenced. Graminoids, however, show a marked degree of similarity in all areas. This is expected, as grasses and sedges tend to be more abundant and perhaps more diversified where wet grass and sedge meadows predominate in the Arctic (Tieszen 1978). The number of low shrub species is slightly higher at Nunivak Island than at the Sadlerochit study site, perhaps due to the lower latitude.

It may be more pertinent to examine the species diversity of those plant genera used by muskoxen. The Sadlerochit River area had a greater species richness of important forage genera such as _Salix_, _Astragalus_, _Hedysarum_ and _Lupinus_ (Table 8). This factor is crucial

Table 8. Comparison of vascular species richness at four Alaskan locations. Data from Prudhoe Bay and Barrow are from Murray and Murray (1978) and data from Nunivak Island are from Bos (1967).

	Species richness							
	Sadlerochit R.		Prudhoe Bay		Barrow		Nunivak Is.	
Plant category	no. species	%	no. species	%	no. species	%	no. species	%
graminoids	40	22.9	48	29.1	40	30.3	43	27.0
forbs	114	65.5	107	64.8	82	62.1	97	61.0
low shrubs	8	4.5	3	1.8	3	2.2	11	6.9
shrubs	12	6.8	7	4.2	7	5.3	8	5.0
Total	174	99.7	165	99.9	132	99.9	159	99.9
Plant genus	no. species		no. species		no. species		no. species	
Salix	10		7		7		6	
Astragalus	3		2		2		2	
Oxytropis	5		5		0		1	
Hedysarum	2		0		1		0	
Lupinus	1		0		0		0	

since a high diversity of plant species provides the grazer with a greater variety of resources (Whittaker 1975). Since forage values of species will differ, an abundance of species available for grazing will allow for greater selection of high quality food throughout the growing season. Phenological differences in growth patterns of plant species means more uniform availability of forage of high quality where species richness is high. Because different plants vary in the proportion of stems, leaves and seeds, and because these structures vary in chemical composition, some of the differences in palatability are due to plant part effects (Van Dyne et al. 1980). Some plants contain noxious substances such as alkaloids, phenolics and tannins which were once considered to be incidental by-products of metabolism. These secondary compounds may be located in greater concentration in different plant parts, such as seeds and old leaves. More recently, substantial evidence shows that these chemicals exist and turn over at a rapid rate, which indicates that they are tied to primary metabolic functions in plants (Whittaker 1970, Seigler and Price 1976). Many of these compounds arise from common substances such as acetic acid and basic amino acids (Whittaker and Feeny 1971). When ingested, these secondary constituents are often either toxic or may inhibit metabolic processes such as digestion. By avoiding those plant parts with the highest concentration of secondary compounds, or by taking small quantities of a noxious plant and thereby diluting toxins with other forage, the herbivore may feed successfully on nutritious yet potentially harmful forage.

In summary, the Sadlerochit River area offers a diverse flora which is nutritious and abundant. A combination of these factors allows muskoxen to improve the quality of their diet and may be responsible for the observed high muskox productivity.

CONCLUSIONS

Sadlerochit Study Area

Since their release in 1969 and 1970, localized muskox populations have become established in the ANWR and are increasing rapidly (Jingfors and Klein in prep.). Several factors have contributed to their increase.

Observations of muskoxen in the Sadlerochit River study area indicated that they are feeding on nutritious and abundant forage species, which may explain the herd's high productivity. The fact that muskoxen have consistently used the Sadlerochit River drainage in preference to adjacent areas since the 1969 transplant is also evidence that it is good quality habitat. The diverse flora in the study area offers a wide array of species as forage for muskoxen, thus allowing them to select preferred forage such as willows and forbs. Other muskox herds in the ANWR have had lower productivities than those in the Sadlerochit drainage (Roseneau and Stern 1974, Bente 1977). Fecal analyses showed that muskoxen in the Jago and Tamayariak drainages have a higher dependency on sedges and grasses for their nutritive needs. Willow was not abundant in these areas and under these circumstances muskoxen may be subsisting on only moderate range resulting in low population numbers. The Jago and Tamayariak muskoxen also wander more and are less consistent in their use of a particular area (W. Audi pers. comm.). Muskox productivity is often erratic in the Canadian Arctic (Tener 1965, Jingfors 1980) where willow and forbs do not predominate, again suggesting that a diverse flora is an indicator of good quality range. The high use of willow by muskoxen is particularly intriguing since willow dry matter digestibility (DMD) for reindeer has been reported to be lower than for sedges (Person *et al*. 1980). Person *et al*. reported that the *in vitro* DMD, using reindeer rumen liquor, for *Salix pulchra* (=*planifolia*) was 20.1 % where the *in vitro* DMD for *Carex aquatilis* was 59.0 %. They suggested that this low digestibility for willow may be due to an accumulation of digestive inhibitors in the rumen and that a willow diet diluted with other species might promote digestibility. Alaskan muskoxen respond with high productivity when on a willow diet, perhaps because they are better able to counteract toxins which may accumulate in the digestive tract.

Riparian Habitat is heavily used by the Sadlerochit muskoxen. Jingfors (1980) showed that these habitats are used in slightly greater proportion than their occurrence in the study area. Since Riparian Habitat covered only 20 % of the Sadlerochit drainage this indicates that muskoxen are selecting riverine vegetation types during the summer. Tussock Meadow was also selected for, but often it was used in association with adjacent Riparian and Creek Willow vegetation types.

In the future, muskoxen in the ANWR are likely to be distributed in the following manner. Populations may centralize in the few drainages, such as the Sadlerochit River, that provide optimal habitat. Other river drainages may include the Canning, Aichilik and Kongakut Rivers where introduced muskoxen have been sighted in the past and which are all characterized by dense growths of willow. Moderate to low numbers of muskoxen may use other riparian areas and narrow creek drainages where willow grows in small thickets. Although upland tundra, such as Tussock Meadow and Dry Ridge, may be used occasionally, especially in late May, large expanses of tundra isolated from riparian drainages will probably see little or no use by muskoxen. Rather than dispersing into upland tundra of low productivity, muskoxen are more likely to emigrate south into the Brooks Range, east into Canada and west across the Canning River out of the ANWR.

The high productivity of muskoxen in the Sadlerochit River study area is presumably a product of low predation and a climate which does not limit winter habitat use, combined with vegetation apparently providing an adequate amount of good quality forage. Low predation levels may help to explain the initial success of muskoxen in the ANWR. Wolves, the most significant predator of muskoxen, have been scarce on the Coastal Plain and northern foothills of the ANWR. Brown bears, less important as predators but responsible for muskox mortality on the Seward Peninsula, Alaska, have not been abundant in the Sadlerochit River study area. Precipitation in the arctic is rarely greater than 150 $mm \cdot yr^{-1}$, and much of this falls as rain and mist during the warmer months. Snowfall is low (see Figure 2), although strong winds pile the snow into deep drifts in gullies and depressions. Wind also exposes vegetation on slopes where muskoxen may find foraging easier than digging through deep drifts. Low temperatures throughout the winter months reduce the chance of icing as a result of thaws. Nunivak Island, in contrast, has a maritime climate with a mean January precipitation of 21.3 mm of rain and 269.2 mm of snow and sleet (Bos 1967). Bos reports a mean temperature for January of -11 C. Muskoxen may experience heavy mortality when ice crusts and deep snow lie directly over vegetation (Lent 1978). Winter conditions restrict muskoxen to the outer perimeter of Nunivak Island where wind reduces snow cover, and foraging is presumably easier (Bos 1967, Spencer and Lensink 1970, Lent and Knutson 1971).

Interspecific Competition

Competition occurs when two species simultaneously seek an essential resource that is in limited supply, such as food or a place to live, hide or breed (Mayr 1970). If two species are competing for a resource that is in short supply, both would benefit by evolving differences that tend to reduce competition (Krebs 1978).

Potential vertebrate competitors with muskoxen for food are caribou, moose, brown bears, ptarmigan and small mammals (ground squirrels, tundra voles, red-backed voles, brown and collared lemmings).

Bears graze on above-ground plant tissues, but due to their low densities in the study area they are not important competitors with muskoxen for food. Brown bears were observed digging and feeding on the roots of *Hedysarum mackenzii* in riparian areas. This plant is an important muskox forage species; however bears often leave root material which allows for regrowth of the plants.

Competition between muskoxen and caribou was minimal due to temporal and spacial separation. Caribou arrived in the Sadlerochit River area in mid- to late May in small bands of 2 to 10 animals, were abundant in June (200-800 individuals seen per day) and had left the area by early July. While in the Sadlerochit River area, caribou, mostly cows with new calves, wandered north-northwesterly as part of their post-calving aggregation movement. They were observed eating Eriophorum vaginatum, Salix pulchra and Carex aquatilis. Plant phenology in the early summer of 1979 was approximately ten days earlier than in 1977 and 1978 and caribou were observed feeding on forbs growing in the riparian vegetation types. In previous years these areas were too flooded and icy at this time to support plant growth. In May and June 1979, caribou fed heavily on Oxytropis maydelliana, an important muskox food species. However, at this time the muskoxen were in tussock meadows 8-9 km from the river feeding on willows (Salix planifolia) and Eriophorum vaginatum. By the time the muskoxen had returned to the river the caribou had left the area and the forbs they had fed on had largely regrown, as the caribou had not grazed below the meristem of the plants. Very little evidence of the previous grazing by caribou was apparent. However, since they were observed feeding on the same plant species, future competition for resources is likely to occur between caribou and muskoxen.

In the vicinity of Sadlerochit Springs, there was much evidence of moose browsing on willow, and on a few occasions moose were seen further north along the river. Although the willow near the springs, primarily *Salix alaxensis*, showed heavy use by moose, this apparently did not limit the availability of forage for muskoxen.

In spite of the heavy bud use by ptarmigan, the effects of their feeding are probably not great because willow is so abundant and many of the shrubs are protected by snow. Ptarmigan were observed feeding in early May 1978 on willow buds and twigs made available under the snow by cratering by muskoxen. Availability of summer forage may be reduced if a large number of buds are removed in the winter, but a small amount of buds removed may even stimulate new sprouting. In late winter and spring, when ptarmigan are numerous, muskoxen do not depend solely on willow for nutrition but also eat *Eriophorum vaginatum*.

Ground squirrels are active only during the summer and feed on willow, graminoids and some forbs, such as

Polygonum bistorta, also eaten by muskoxen. These animals are especially abundant along the river bluffs where the dry, sandy soil offers good denning habitat. Ground squirrels may compete for food in the summer, but they also contribute to floral diversity. Their burrowing in the banks redistributes soil and provides disturbed areas for pioneering species of *Oxytropis*, *Astragalus*, *Arctagrostis* and other plants which are fed upon by muskoxen. They also add nutrients to the soil through their excretory products and relocate nutrients and seeds through their foraging habits.

Tundra voles appear to be colonial and make moderately heavy use of willow and lupine and also girdle some willow in winter. This could limit availability of muskox forage in localized areas, although it is probably not too important under normal population levels of voles. Other small mammals feed primarily on plants not particularly important to muskoxen (*Carex aquatilis* and *Eriophorum angustifolium*), and therefore probably have little effect on availability of preferred muskox forage.

Potential Impacts of Resource Development

Muskoxen are one of the few species that remain active in the Arctic throughout the entire year. During winter, the abundance and nutritive quality of forage is low. Availability of food in winter depends upon snow cover and may fluctuate from year to year. During winter, northern ungulates are normally in a negative nutritive relationship with their environment and are dependent upon stored fat reserves to supplement the limitations in the available forage. Muskoxen are particularly vulnerable to harassment (Miller and Gunn 1979). They are unique and uncommon animals and the increased possibility of resource development on the north slope of the ANWR increases the likelihood that they will be the objects of disturbance. In the flat terrain of their environment and particularly in winter when snow cover renders the landscape a nearly uniform white, they are extremely visible. Low flying aircraft may approach too closely while attempting to observe or photograph the animals. Increased energy expenditure from this type of disturbance may be enough to put some animals in a critical physiological state.

The effect of man-made obstructions as a result of oil development on wildlife populations has been dealt with by Child (1973), Klein (1972), Cameron and Whitten (1976) and Roby (1978 a). In particular, caribou populations were studied in the vicinity of the Trans-Alaska Pipeline System

(TAPS). The most negative reactions were from cows with calves, which avoided the TAPS corridor. Roads, railroads, powerlines and hydroelectric projects have been observed to affect movements of reindeer in Scandinavia (Klein 1972).

Finally, destruction of habitat used by muskoxen could impact herd movements and survival. The vegetation along the gravel outwashes of the Sadlerochit River was found to be important to muskoxen. Riparian areas are likely to suffer disturbance because they are a major source of gravel which is required for work pads, roads, airfields and pipelines, and river valleys are often the most favored routes for roads and pipelines. Muskoxen have regularly calved in late May in an area about 10 km east of Marsh Creek, an area geologists claim is rich in oil deposits (Jingfors 1980). Displacement of muskoxen from the preferred riparian habitats due to harassment or habitat alteration through gravel removal would likely lead to reduction or possibly loss of the present herds because of lower vegetative productivity in other habitats. Oil exploration would bring more people to an unpopulated area with associated disturbance to the muskoxen and perhaps leading to increased tourism and illegal hunting.

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APPENDIX A

Vascular plant species collected at the base camp location, Sadlerochit River, 1978 and 1979. Plant families are organized according to Hultén (1968). Species of the Salicaceae are named according to Viereck and Little (1972).

GRAMINAE

Agropyron boreale (Turcz.) Drobov subsp. *alaskanum* (Scribn. and Merr.) Melderis

A. boreale (Turcz.) Drobov subsp. *boreale*

A. macrourum (Turcz.) Drobov

Alopecurus alpinus Sm. subsp. *alpinus*

Arctagrostis latifolia (R. Br.) Griseb. var. *latifolia*

Arctophila fulva (Trin.) Anderss.

Bromus pumpellianus Scribn. var. *arcticus* (Shear) Pors.

B. pumpellianus Scribn. var. *pumpellianus*

Calamagrostis inexpansa Gray

Deschampsia caespitosa (L.) Beauv. subsp. *orientalis* Hult.

Dupontia fischeri R. Br. subsp. *psilosantha* (Rupr.) Hult.

Festuca baffinensis Polunin

F. rubra L. coll.

"*F. vivipara*"

Hierochloe alpina (Sw.) Roem. and Schult.

Poa alpina L.

P. lanata Scribn. and Merr.

P. paucispicula Scribn. and Merr.

Puccinellia andersonii Swallen

Trisetum spicatum (L.) Richter subsp. *spicatum*

CYPERACEAE

Carex aquatilis Wahlenb. subsp. *aquatilis*

C. aquatilis Wahlenb. subsp. *stans* (Drej.) Hult.

C. bigelowii Torr.

C. Krausei Boeck.

C. podocarpa C.B. Clarke

C. saxatilis L. subsp. *laxa* (Trautv.) Kalela

C. scirpoidea Michx.

Eriophorum angustifolium Honck. subsp. *triste* (T. Fries) Hult.

E. scheuchzeri Hoppe var. *scheuchzeri*

E. vaginatum L. subsp. *spissum* (Fern.) Hult.

Kobresia myosuroides (Vill.) Fiori and Paol.

K. simpliciuscula (Wahlenb.) Mack.

JUNCACEAE

Luzula confusa Lindeb.

L. tundricola Gorodk.

Juncus arcticus Willd. subsp. *alaskanus* Hult.

J. castaneus Sm. subsp. *castaneus*

J. triglumis L. subsp. *albescens* (Lange) Hult.

LILIACEAE

Lloydia serotina (L.) Rchb.

Tofieldia coccinea Richards.

T. pulsilla (Michx.) Pers.

SALICACEAE

Salix alaxensis (Anderss.) Cov.

S. arbusculoides Anderss.

S. arctica Pall.

S. brachycarpa Nutt. subsp. niphoclada (Rydb.) Argus

S. glauca L.

S. lanata L. subsp. richardsonii (Hook.) A. Skwortz.

S. ovalifolia Trautv.

S. phlebophylla Anderss.

S. planifolia Pursh subsp. pulchra (Cham.) Argus

S. reticulata L.

BETULACEAE

Betula nana L. subsp. exilis (Sukatsch.) Hult.

POLYGONACEAE

Oxyria digyna (L.) Hill

Polygonum bistorta L. subsp. plumosum (Small) Hult.

P. viviparum L.

Rumex arcticus Trautv.

CARYOPHYLLACEAE

Cerastium beeringianum Cham. and Schlecht. var. beeringianum

C. beeringianum Cham. and Schlecht. var. grandiflorum (Fenzl) Hult.

Melandrium affine J. Vahl

M. apetalum (L.) Fenzl subsp. arcticum (E. Fries) Hult.

Minuartia arctica (Stev.) Aschers. and Graebn.

M. biflora (L.) Schinz and Thell.

Sagina intermedia Fenzl

Silene acaulis L. subsp. acaulis

Stellaria crassifolia Ehrh.

S. edwardsii R. Br.

S. laeta Richards.

S. longipes Goldie

S. monantha Hult.

Wilhelmsia physodes (Fisch.) McNeill

RANUNCULACEAE

Aconitum delphinifolium DC. subsp. paradoxum (Rchb.) Hult.

Anenome parviflora Michx.

A. richardsonii Hook.

Caltha palustris L. subsp. arctica (R. Br.) Hult.

Delphinium brachycentrum Ledeb.

Ranunculus gmelini DC. subsp. gmelini

R. hyperboreus Rottb. subsp. hyperboreus

R. nivalis L.

R. pallasii Schlecht.

R. pedatifidus Sm. subsp. affinis (R. Br.) Hult.

PAPAVERACEAE

Papaver lapponicum (Tolm.) Nordh. subsp. porsildii Knaben

P. macounii Greene

CRUCIFERAE

Arabis lyrata L. subsp. kamchatica (Fisch.) Hult.

Cardamine bellidifolia L.

C. hyperborea O.E. Schulz

C. pratensis L. subsp. angustifolia (Hook.) O.E. Schulz

Cochlearia officinalis L. subsp. arctica (Schlecht.) Hult.

Descurainia sophoides (Fisch.) O.E. Schulz

Draba hirta L.

D. lactea Adams

D. longipes Raup

D. macrocarpa Adams

D. nivalis Liljebl.

D. pilosa DC.

Eutrema edwardsii R. Br.

Parrya nudicaulis (L.) Regel subsp. septentrionalis Hult.

CRASSULACEAE

Sedum rosea (L.) Scop. subsp. integrifolium (Raf.) Hult.

SAXIFRAGACEAE

Boykinia richardsonii (Hook.) Gray

Parnassia kotzebuei Cham. and Schlecht.

P. palustris L. subsp. *neogaea* (Fern.) Hult.

Saxifraga bronchialis L. subsp. *funstonii* (Small) Hult.

S. caespitosa L.

S. cernua L.

S. davurica Willd. subsp. *grandipetala*

S. exilis Steph.

S. hieracifolia Waldst. and Kit.

S. hirculus L.

S. nivalis L.

S. oppositifolia L. subsp. *oppositifolia*

S. punctata L. subsp. *nelsoniana* (D. Don) Hult.

S. rivularis L. var. *rivularis*

S. tricuspidata Rottb.

ROSACEAE

Dryas integrifolia M. Vahl subsp. *integrifolia*

Potentilla biflora Willd.

P. fruticosa L.

P. palustris (L.) Scop.

P. uniflora Ledeb.

Rubus arcticus L. subsp. *acaulis* (Michx.) Focke

R. chamaemorus L.

LEGUMINOSAE

Astragalus alpinus L. subsp. *alpinus*

A. eucosmus Hornem. subsp. *sealei* (Lepage) Hult.

A. umbellatus Bunge

Hedysarum alpinum L. subsp. *americanum* (Michx.) Fedtsch.

H. mackenzii Richards.

Lupinus arcticus S. Wats.

Oxytropis arctica R. Br.

O. borealis DC.

O. deflexa (Pall.) DC. var. *foliosa* (Hook.) Barneby

O. maydelliana Trautv.

O. nigrescens (Pall.) Fisch. subsp. *pygmaea* (Pall.) Hult.

ONAGRACEAE

Epilobium latifolium L.

E. palustre L.

HALORAGACEAE

Hippuris tetraphylla L.f.

PYROLACEAE

Pyrola asarifolia Michx. var. *purpurea* (Bunge) Fern.

P. grandiflora Radius

EMPETRACEAE

Empetrum nigrum L. subsp. *hermaphroditum* (Lange) Bocher

ERICACEAE

Andromeda polifolia L.

Arctostaphylos rubra (Rehd. and Wilson) Fern.

Cassiope tetragona (L.) D. Don subsp. *tetragona*

Ledum palustre L. subsp. *decumbens* (Ait.) Hult.

Rhododendron lapponicum (L.) Wahlenb.

Vaccinium uliginosum L. subsp. *microphyllum* Lange

V. vitis-idaea L. subsp. *minus* (Lodd.) Hult.

PRIMULACEAE

Androsace chamaejasme Host subsp. *lehmanniana* (Spreng.) Hult.

Dodecatheon frigidum Cham. and Schlecht.

GENTIANACEAE

Gentiana propinqua Richards. subsp. *propinqua*

G. prostrata Haenke

POLEMONIACEAE

Polemonium acutiflorum Willd.

P. boreale Adams subsp. *boreale*

SCROPHULARIACEAE

Castilleja caudata (Pennell) Rebr.

Lagotis glauca Gaertn. subsp. *minor* (Willd.) Hult.

Pedicularis capitata Adams

P. kanei Durand subsp. *kanei*

P. langsdorffii Fisch. subsp. *arctica* (R. Br.) Pennell

P. sudetica Willd. subsp. *albolabiata* Hult.

P. verticillata L.

VALERIANACEAE

Valeriana capitata Pall.

COMPOSITAE

Achillea borealis Bong.

Antennaria friesiana (Trautv.) Ekman subsp. alaskana (Malte) Hult.

Arnica alpina (L.) Olin subsp. angustifolia (M. Vahl) Maguire

Artemisia arctica Less. subsp. comata (Rydb.) Hult.

A. glomerata Ledeb.

A. tilesii Ledeb. subsp. tilesii

Aster sibiricus L.

Crepis nana Richards. var. nana

Erigeron eriocephalus J. Vahl

E. humilis Graham

Petasites frigidus (L.) Franch.

Saussurea viscida Hult. var. yukonensis (Pors.) Hult.

Senecio atropurpureus (Ledeb.) Fedtsch. subsp. frigidus (Richards.) Hult.

S. lugens Richards.

S. resedifolius Less.

Taraxacum ceratophorum (Ledeb.) DC.

APPENDIX B

List of A_x and G_x values used in calculating the preference ratios (PR).

$$PR = RU_x/RA_x, \text{ where: } RU_x = g_x/\sum_{i=1}^{n} g_i \text{ , } RA_x = a_x/\sum_{i=1}^{n} a_i$$

and

$$g_x = G_x/45 \text{ m2}, \; a_x = A_x/45 \text{ m}^2$$

Species	A_x (m2)	G_x (m2)
30 May 1979		
Carex bigellowii	4.47	0.01
Eriophorum vaginatum	8.50	0.07
31 May 1979		
Dryas integrifolia	15.50	2.28
Kobresia simpliciuscula	1.07	0.09
Luzula tundricola	1.87	0.11
Oxytropis nigrescens	1.22	0.06
Pedicularis kanei	0.12	0.01
Salix phlebophylla	5.20	0.13
grass	1.15	0.02
18 June 1979		
Eriophorum vaginatum	6.60	0.23
1 July 1979		
Lupinus arcticus	2.40	0.04
Salix alaxensis	5.52	0.13
6 July 1979		
Carex bigellowii	2.67	0.02
Eriophorum vaginatum	7.85	0.02
Pedicularis kanei	0.32	0.03
Petasites frigidus	1.75	0.04

Species	A_x (m2)	G_x (m^2)
Polygonum bistorta	2.02	0.02
Salix pulchra	6.65	0.13
7 July 1979		
Astragalus alpinus	0.70	0.06
A. umbellatus	1.80	0.06
Carex bigellowii	5.25	0.01
Lagotis glauca	0.97	0.02
Oxytropis maydelliana	0.25	0.07
Parrya nudicaulis	0.95	0.06
Pedicularis kanei	0.70	0.03
Polygonum bistorta	1.05	0.01
21 July 1979		
Astragalus alpinus	2.35	0.14
Epilobium latifolium	3.52	0.05
Oxytropis maydelliana	0.22	0.02
Pedicularis sudetica	0.05	0.02
P. verticillata	0.17	0.01
Salix alaxensis	3.22	0.10
S. glauca	0.77	0.03
grass	2.42	0.01
27 July 1978		
Astragalus alpinus	2.07	0.10
Castilleja caudata	1.57	0.05
Lupinus arcticus	1.90	0.07
Oxytropis borealis	3.30	0.01
O. maydelliana	0.32	0.01
Pedicularis verticillata	1.15	0.03
Salix alaxensis	15.12	0.82
S. brachycarpa	1.47	0.07
S. glauca	5.17	0.02
28 July 1978		
Artemisia arctica	2.27	0.04
A. tilesii	0.50	0.01
Astragalus alpinus	12.25	0.41
Epilobium latifolium	2.37	0.08
Hedysarum mackenzii	1.35	0.31
Oxytropis borealis	1.22	0.01
O. maydelliana	0.70	0.05
Pedicularis verticillata	0.75	0.05

Species	A_x (m2)	G_x (m2)
Salix alaxensis	2.17	0.06
S. brachycarpa	0.15	0.01
S. glauca	0.62	0.03
grass	5.22	0.03
1 August 1979		
Astragalus alpinus	2.85	0.05
Castilleja caudata	0.92	0.05
Hedysarum mackenzii	0.62	0.03
Salix alaxensis	10.55	0.56
S. brachycarpa	1.12	0.01
S. glauca	5.50	0.08
grass	5.02	0.01
1 August 1979		
Astragalus alpinus	8.65	0.16
Castilleja caudata	1.12	0.04
Epilobium latifolium	1.47	0.02
Oxytropis maydelliana	0.77	0.01
Salix alaxensis	2.47	0.03
15 August 1979		
Astragalus alpinus	7.55	0.03
Hedysarum mackenzii	0.22	0.02
Salix alaxensis	6.10	0.19
S. glauca	6.17	0.10